THE ORIGIN, INTERRELATIONSHIP AND DISTRIBUTION OF SOUTHERN AFRICAN RAJIDAE (CHONDRICHTHYES, BATOIDEI)

By

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(With 59 figures and 4 tables)

[*Ms. accepted* 27 *March* 1972]

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Introduction

Skates, which show the greatest species diversity among elasmobranch fishes, are included in the family Rajidae, and are characterized by their dorso-ventrally flattened, rhomboidal disc, moderately slender tail, usually with two dorsal fins and a membraneous caudal fin, and lack of serrate tail spines. Although they are regularly taken in bottom trawls, together with stockfish (*Merluccius capensis*), kingklip (*Genypterus capensis*), jacopever (*Helicolenus dactylopterus*) and monkfish (*Lophius piscatorius*), they form a small proportion of the total catch (0,001–0,075%) by South African commercial trawlers, and their landed weight has shown a sharp decline from 131 814 lb in 1963 to 14 199 lb in 1965 (Division of Sea Fisheries Report, 1968).

In order to clarify the position of the Rajidae within the southern African ichthyofaunal complex, a research programme was instigated by Dr F. H. Talbot, formerly of the South African Museum, to investigate the systematics, distribution and phylogeny of the group. Hulley (1966, 1969, 1970) has revised the Rajidae of the west and south coasts of southern Africa, at the species level, while Wallace (1967) has investigated the east coast species. From this, it appears that natural relationships between the species are evident, suggesting a regrouping of the *Raja* species at the generic or subgeneric level.

Because of difficulties associated with individual variation, Ishiyama (1952, 1958, 1968) adopted a new approach to rajid systematics, employing characteristics of the clasper, structure of the neurocranium, number of

Ann. S. Afr. Mus. **60** (1), 1972: 1–103, 59 figs, 4 tables.

intestinal valves and valves in the *conus arteriosus*, and the vertebral count, as well as standard morphometric procedures, and has established several new genera and subgenera. Stehmann (1970) has followed this method, supplemented by investigations on the ampullae of Lorenzini and number of pseudobranchial folds in the spiracle, and has proposed 6 subgenera within the genus *Raja* in the eastern North Atlantic. It appears, however, that of these characters only the anatomy of the clasper, shape of the skull and rostral cartilages, and vertebral count prove to be definite key characters.

These methods have been adopted in this investigation, not only for comparison of southern African species with their European counterparts, but also for establishing interrelationships within the family and the possible origin of the southern African rajid fauna.

The scheme of classification followed in this paper is that of Bigelow & Schroeder (1953).

This work formed part of a thesis submitted for the degree of Ph.D. at the University of Cape Town in October 1971, and the author is indebted to the University, and particularly the Zoology Department, for permission to publish the results.

MATERIALS AND METHODS

489 specimens, including the types of the following species were examined in detail: *Cruriraja parcomaculata*, *C. triangularis*, *Raja doutrei*, *R. pullopunctata*, *R. stenorhynchus*, *R. lanceorostrata*, *R. springeri*, *R. alba*, *R. spinacidermis*, *R. miraletus*, *R. clavata*, *R. straeleni*, *R. robertsi*, *R. radiata*, *R. wallacei*, *R. caudaspinosa*, *R. ravidula*, *R. leopardus*, *R. confundens*, *R. dissimilis*, *Bathyraja smithii*. All material in the collections of the J. L. B. Smith Institute of Ichthyology, Grahamstown, and the Oceanographic Research Institute, Durban, has been re-examined.

Material collected in the South Atlantic by the *Discovery*, FFS *Walther Herwig* and the Belgian South Atlantic Expedition was seen during visits to London, Hamburg and Brussels, while specimens from the eastern North Atlantic, housed in the British Museum (Natural History), Institut für Seefischerei, Institut Royal des Sciences Naturelles de Belgique, and Muséum National d'Histoire Naturelle were examined, including specimens from Sierra Leone and Senegal.

Specimens of *Cruriraja rugosa* and *Anacanthobatis americanus* were obtained from the National Museum of Natural History, Washington, for comparative anatomical studies, and this institution also supplied X-ray photographs of *Raja garmani*, *R. oregoni*, *Pseudoraja fisheri*, *P. atlantica* and *Gurgesiella furvescens*. Further X-ray photographs of *Raja flavirostris*, *Psammobatis extenta*, *P. microps*, *P. lima* and *P. scobina* were supplied by the British Museum (Natural History), of *Raja straeleni* by the Institut für Seefischerei and of *Raja miraletus* and *R. straeleni* by the Institut Royal des Sciences Naturelles de Belgique.

The pelvic girdles of southern African Rajoidea have been examined by means of X-ray photography and the drawings made from the negatives have been scaled to the same width for comparative purposes. X-ray photographs of the pelvic girdle of *Springeria ori* did not prove to be completely satisfactory, but it appears that this is not unlike the girdle of *Anacanthobatis marmoratus*.

Claspers from adult males of the following species have been examined in detail by dissection: *Cruriraja parcomaculata*, *C. triangularis*, *C. rugosa*, *Raja doutrei*, *R. pullopunctata*, *R. lanceorostrata*, *R. alba*, *R. caudaspinosa*, *R. miraletus*, *R. clavata*, *R. straeleni*, *R. dissimilis*, *R. confundens*, *R. leopardus*, *R. wallacei*, *Bathyraja smithii*, *Anacanthobatis marmoratus*, *A. americanus*, *Rhinobatos annulatus*, *Myliobatis cervus*. All material had been preserved in either 70% ethyl alcohol or 5% formalin. Where possible several dissections were made for the particular species. Brief examinations of the external morphology of the claspers of other South African Batoidei have been made for comparative purposes: the species include *Rhinobatos ocellatus*, *Gymnura javanica*, *Mobula diabolus*, *Dasyatis thetidis*, *Urotrygon daviesi*, *Heteronarce garmani* and *Torpedo nobiliana*.

Claspers of European *Raja clavata*, *R. radiata*, *R. miraletus* and *R. batis* and the South American species *R. flavirostris* have also been dissected for comparative purposes.

Vertebral counts were facilitated by the use of X-ray photography. The number of predorsal caudal vertebrae (Vprd) has been taken as the number of caudal vertebrae up to the origin of the first dorsal fin (Ishiyama 1952; Krefft 1968*a*); the number of trunk vertebrae (Vtr) and total count (VΣ) are given according to Krefft (1968*a*). Vprd counts were not possible in *Anacanthobatis marmoratus*, *A. americanus* and *Springeria ori*, as these species lack dorsal fins.

Although Bigelow & Schroeder (1953) have employed X-ray photography in examination of the snout, this method has not been used in this study, because of the small extent of calcification of the rostral cartilages and appendices (Ishiyama & Hubbs 1968). In all cases, the rostral cartilages and rostral appendices were examined by dissection, preserved material being soaked in a weak (2%) solution of NaOH, according to the method of Stehmann (1970). Where possible, the neurocrania were also examined in this way, but in several cases, *Cruriraja triangularis*, *Raja lanceorostrata*, *R. springeri*, *R. stenorhynchus*, *R. straeleni*, *R. robertsi*, *R. dissimilis*, *R. ravidula*, *R. wallacei* and *R. spinacidermis*, dissection of neurocrania could not be made. These were examined by X-ray photography. The neurocrania of *Anacanthobatis marmoratus* and *Springeria ori* could not be examined by dissection, while X-ray photography gave poor results. The cranial characters of these species are therefore not included in the study. Nerve foramina were affirmed by dissection.

Pelvic Girdle and Clasper Structure

PELVIC GIRDLE

The pelvic bar is made up of a pair of anlage, which arise together with the basals and peripheral radials in a continuous procartilaginous rudiment (Balfour 1881). While the anlage remain separate in the Holocephali, they fuse to form a single element, situated in front of the cloaca in Elasmobranchii. Subdivision of the anlage in *Cladodus* suggests that the pelvics arose from a fusion of originally independent basal fin elements.

Contrary to Wiedersheim's theory (1892), Braus (1902) has shown that the pelvic girdle consists of a transverse, bow-like cartilage, from which plate-like girdles, e.g. *Chlamydoselachus* (Daniel 1934: fig. 85), may be derived. The transverse band of cartilage is divisible into a median ischiopubic region and lateral iliac regions, which may be slightly expanded and which are penetrated by obturatorial nerve foramina for the passage of the diazonal nerves. The number of foramina may vary considerably, from one in *Squalus acanthias* to eight in *Chlamydoselachus* (Kälin 1939).

Transverse pelvic bars occur in all batoid families, except the Dasyatidae, Myliobatidae and Mobulidae (Garman 1913: figs 53, 54), in which they are anteriorly arched and bear a single, median, prepelvic process—*processus*

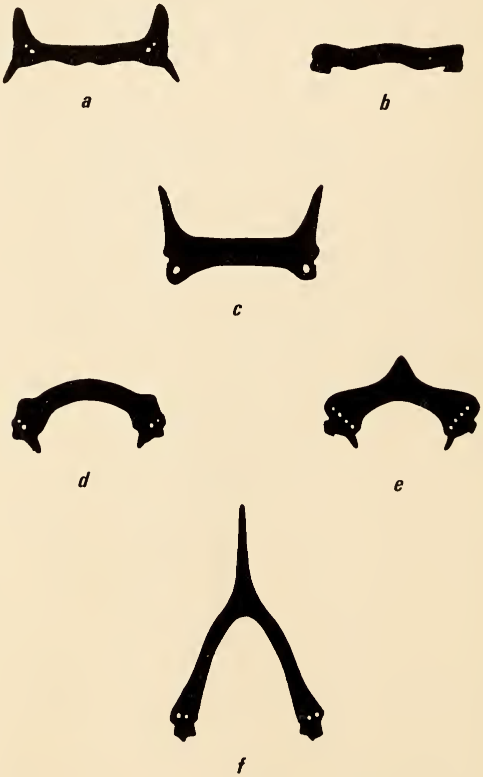

Fig. 1. Pelvic girdles of Batoidei. a. *Rhinobatos* (after Daniel 1934); b. *Platyrhina* (after Garman 1913); c. *Arhynchobatis* (after Garrick 1954); d. *Dasyatis* (after Garman 1913); e. *Myliobatis* (after Garman 1913); f. *Mobula* (after Garman 1913).

praepubicus. However, in the Rhinobatidae, Platyrhinidae, Rajidae, Anacanthobatidae and Arhynchobatidae, a pair of lateral prepelvic processes arise from the antero-lateral edge of the pelvic bar and are directed anteriorly.

Besides the brief references to the pelvic girdle by Garman (1913) and Garrick (1954, 1957), no comparative investigation of the girdle in Rajoidea has been made.

Typically, the girdle is short and bar-like and is expanded laterally at the iliac regions. Arising from the antero-lateral edges of the iliac regions are a pair of prepelvic processes. In the Anacanthobatidae, the iliac regions are more developed, which together with an increase in length of the prepelvic processes, gives the girdle a U-shape. The girdle appears to be of intermediate shape in *Cruriraja* species and in *Arhynchobatis asperrimus* (Garrick 1954: fig. 3), so that the trend in this mode of development is shown by the series *Raja*, *Cruriraja*, *Arhynchobatis* and *Anacanthobatis* (Fig. 2).

The lengths of the prepelvic processes vary considerably; in *Raja* species, their lengths vary from 0,1 to 0,3 of the girdle width; in *Bathyraja smithii*

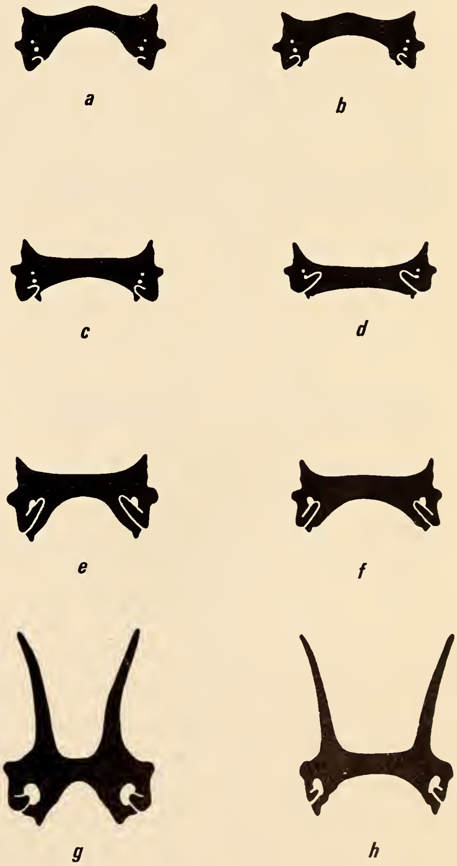

Fig. 2. Pelvic girdles of southern African Rajidae, showing sexual dimorphism. a. *Raja springeri* (male); b. *R. springeri* (female); c. *Raja confundens* (male); d. *R. confundens* (female); e. *Cruriraja parcomaculata* (male); f. *C. parcomaculata* (female); g. *Anacanthobatis marmoratus* (male); h. *A. marmoratus* (female).

about 0,3; in *Cruriraja* species from 0,1 to 0,2; in *Arhynchobatis asperrimus* about 0,3; and in *Anacanthobatis* species from 0,8 to 0,9.

A short, stout, iliac process arises postero-laterally on each side from the dorsal surface of the bar, but this recurves inwards to point anteriorly and terminates in a bluntly rounded point. The iliac region is usually penetrated by two (sometimes more) obturatorial foramina in most species, but in *Cruriraja parcomaculata*, *C. triangularis* and *Anacanthobatis marmoratus* and in the North Atlantic species *Cruriraja rugosa* and *Anacanthobatis americanus*, there is a single foramen on each side (Fig. 4). Garrick (1954: fig. 3) has shown a single foramen in the monotypic *Arhynchobatis asperrimus.*

Sexual dimorphism is evident in the pelvic girdles (Fig. 2), and although it is not particularly marked in *Raja* and *Bathyraja* species, it is noticeable in *Cruriraja*, *Anacanthobatis* and *Springeria.* In these genera, the posterior edge of the ischiopubic region is strongly arched in males, due partly to the increase in size of the iliac regions, while in females the posterior edge is only slightly arched, giving rise to a much more elongate bar between the prepelvic processes. This feature is probably linked with the oviparous behaviour of the suborder.

The 'black-bellied' skates, *Raja doutrei*, *R. stenorhynchus*, *R. springeri*, *R. pullopunctata* and *R. lanceorostrata* (Figs 3 a–e) are unusual in that they show a graded variation in anterior arching of the bar, which is unlike the simple, transverse bar of most other species of *Raja.* This type of arched bar, as has been pointed out above, approximates the condition in the Dasyatidae, Myliobatidae and Mobulidae (Fig. 1). However, in these families there is a single, median, prepelvic process, while in black-bellied skates the paired, lateral processes indicative of the rajid condition, are present.

In the *clavata*-group (Figs 3 g, i, j), which in the eastern South Atlantic consists of the species *Raja clavata*, *R. straeleni* and *R. miraletus*, the prepelvic processes show an increase in length from *Raja straeleni* to *R. clavata.* In the latter species the length of the prepelvic processes approximates to that of *Arhynchobatis asperrimus.* Furthermore, slight anterior arching of the ischiopubic bar is seen in *Raja miraletus* and *R. clavata.*

The girdle of *Bathyraja smithii* (Fig. 3 t) resembles that of *Raja clavata* and *R. miraletus* in the length of the prepelvic processes, but differs in the iliac processes. These are only slightly curved in *Bathyraja smithii*, and so attain a position intermediate between that of *Rhinobatos* (Fig. 1 a) and most typical rajids. It should be noted that a similar condition of the iliac processes is found in *Raja robertsi* (Fig. 3 s), but in this species the prepelvic processes are much shorter than in *Bathyraja smithii*, and the girdle represents a case intermediate between that of *Raja radiata* (Fig. 3 r) and *Bathyraja smithii.*

A straight, transverse bar is found in the species *Raja dissimilis*, *R. ravidula*, *R. confundens*, *R. wallacei*, *R. leopardus*, *R. caudaspinosa* and *R. spinacidermis* (Figs 3 k–q), in which cases there is some variation in the prepelvic length. However, in *Raja wallacei* and *R. caudaspinosa* (Figs 3 n, p), the iliac processes appear to be more strongly developed than in the other species, except *Raja*

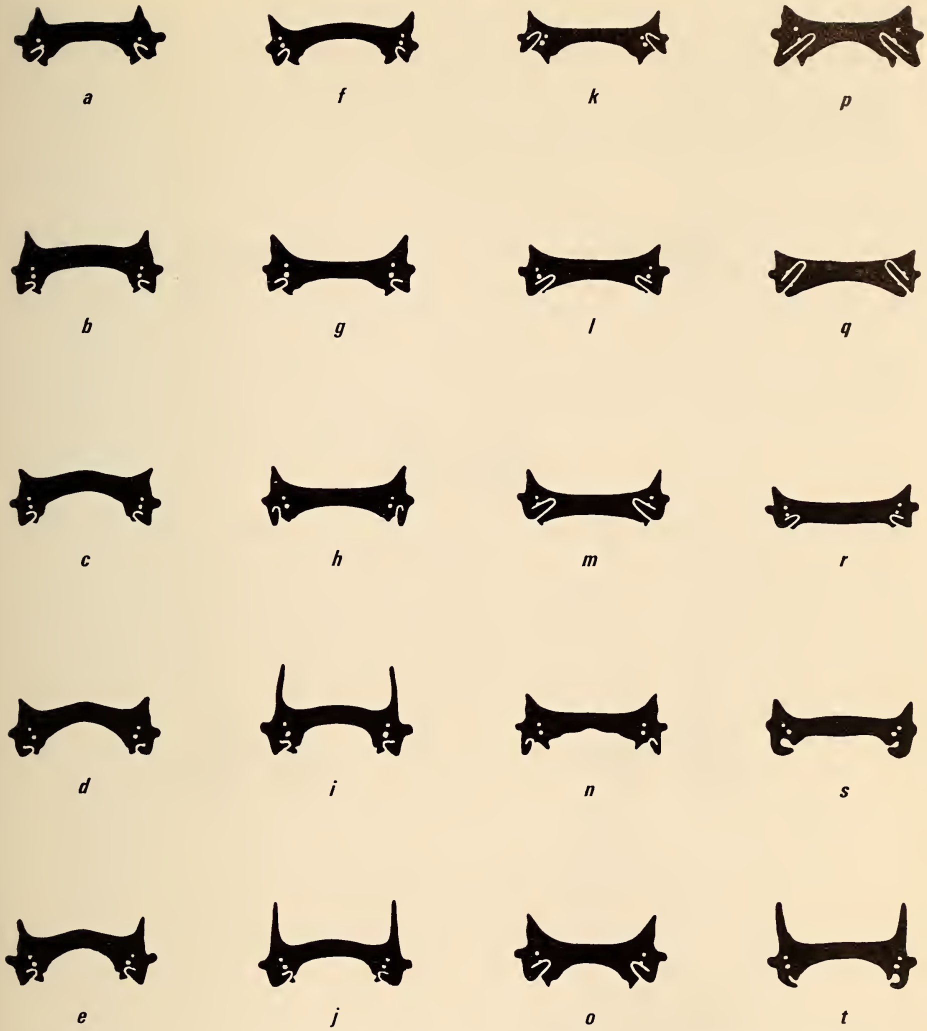

Fig. 3. Pelvic girdles of southern African Rajidae. a. *Raja doutrei*; b. *R. stenorhynchus*; c. *R. springeri*; d. *R. pullopunctata*; e. *R. lanceorostrata*; f. *R. flavirostris* (South American); g. *R. straeleni*; h. *R. alba*; i. *R. miraletus*; j. *R. clavata*; k. *R. dissimilis*; l. *R. ravidula*; m. *R. confundens*; n. *R. wallacei*; o. *R. leopardus*; p. *R. caudaspinosa*; q. *R. spinacidermis*; r. *R. radiata*; s. *R. robertsi*; t. *Bathyraja smithii*.

spinacidermis (Fig. 3 q), which represents the extreme case. In this species the iliac processes extend forward to the anterior edge of the pelvic bar, and in one specimen (the type) the processes extend beyond the edge.

A similar condition is seen in *Cruriraja* species (Figs 4 a–c), where the length of the prepelvic processes approximates that of typical rajids, but where the iliac processes are more massively developed. However, in *Cruriraja parcomaculata*, *C. triangularis* and *C. rugosa*, the iliac processes do not reach the anterior edge of the bar, as they do in *Raja spinacidermis*.

In *Anacanthobatis marmoratus* (Fig. 4 d), *A. americanus* and *Springeria ori*, it is the prepelvic processes which are strongly developed, being almost equal in length to the width of the girdle. On the other hand, the iliac processes are reduced to small, truncate protuberances.

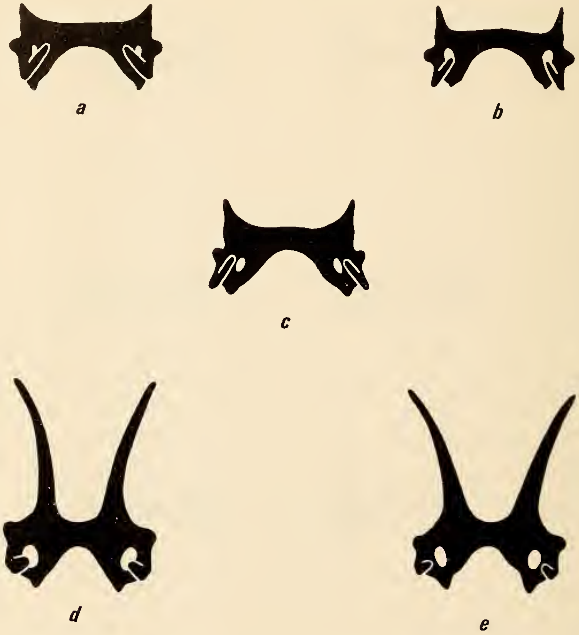

Fig. 4. Pelvic girdles of southern African Rajoidea. a. *Cruriraja parcomaculata*; b. *C. triangularis*; c. *C. rugosa* (North Atlantic); d. *Anacanthobatis marmoratus*; e. *A. americanus* (North Atlantic).

CLASPER STRUCTURE

Although there are major differences in the siphon and clasper gland structure between Selachii and Batoidei (Leigh-Sharpe 1926; White 1937), it is the distal end of the clasper which is important in the systematics of lower taxa. Anatomical investigations on the claspers of European rajids have been made by Petri (1878), Jungersen (1899), Huber (1901), Leigh-Sharpe (1920–6) and Stehmann (1970), while Ishiyama (1958) and Ishiyama & Hubbs (1968) have made detailed studies of the structure and systematic significance of the organ in Japanese rajids. Hulley (1966, 1969) has described the clasper structure of several South African species, and although he has figured the external structure of the claspers in eastern South Atlantic species (1970), detailed comparative anatomical studies of these organs have not been made.

Terminology of external features

Leigh-Sharpe (1920–6) defined most of the terminology used in clasper anatomy, but it can be seen that his use of a particular term is not always constant, since the same cartilaginous element is not always involved. The reason for this is that he dealt only with the external morphology of the organ, without reference to the internal cartilages.

Furthermore, differences in terminology of clasper components as employed by Leigh-Sharpe (1920–6), and by Ishiyama (1958) and Ishiyama & Hubbs (1968), have added to the confusion. In order to standarize, Stehmann (1969) evaluated the terms pseudosiphon, slit, rhipidion and spur, and gave precise definitions for his nomenclature. While the terminology used here is mainly in accordance with his findings, there appears to be confusion in several other structures. A discussion of all problematic components, applicable to southern African Rajidae, follows below:

(1) *pseudosiphon*

Leigh-Sharpe (1921: 361) introduced the term pseudosiphon for *Galeus vulgaris*, defining it as 'a small blindly ending sac, whose wide aperture points in a posterior direction'. He shows that the pseudosiphon is situated on the outer surface of the dorsal lobe of the clasper glans (1921: fig. 2). However, in *Raja* species (*R. clavata*, *R. blanda*, *R. marginata*), he indicates that the pseudosiphon lies on the inner surface of the dorsal lobe. Ishiyama (1958) gives a

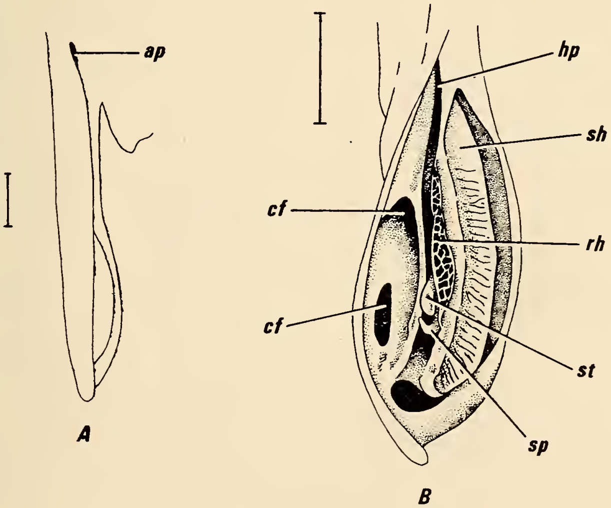

Fig. 5. *Raja lanceorostrata*. A. external view of right clasper from dorsal side; B. lateral view of right clasper opened to show structural features of the glans. Scale 2,0 cm.
cf—cleft; hp—hypopyle; rh—rhipidion; sh—shield; sp—spike; st—sentinel.

similar definition and points out that the pseudosiphon is always related to modifications of the dorsal terminal cartilages.

In 1968, Ishiyama & Hubbs defined the pseudosiphon more precisely, relating it to the degree of development of a single cartilage, the dorsal terminal 1. They point out that a pseudosiphon is indicative of the genus *Bathyraja*.

According to Stehmann (1969), Ishiyama's first definition of the pseudosiphon could be interpreted to mean that the structure could be found either on the outer surface or the inner surface of the dorsal lobe. However, Ishiyama (1958: fig. 3) has shown that the pseudosiphon is situated externally. Further, in his discussion of the slit, he points out that this structure may be related to dorsal terminal cartilages, but (1958: 202) 'has no close relation to the dorsal terminal 1', inferring that the pseudosiphon does have a relationship with that cartilage. Therefore, it appears that there is no distinction between the Ishiyama (1958) definition and the Ishiyama & Hubbs (1968) definition.

In all species investigated in this paper, except those of the genus *Cruriraja*, the dorsal terminal 1 cartilage overlies the other dorsal terminals, so that if a pseudosiphon is related directly to the dorsal terminal 1, then it must be situated externally, on the outer surface of the dorsal lobe of the glans. It would appear, therefore, that the structure referred to as a pseudosiphon by Leigh-Sharpe (1920–6) in the species *Raja clavata*, *R. blanda* and *R. marginata*, which occurs on the inner surface of the dorsal lobe, should be given a new name. In

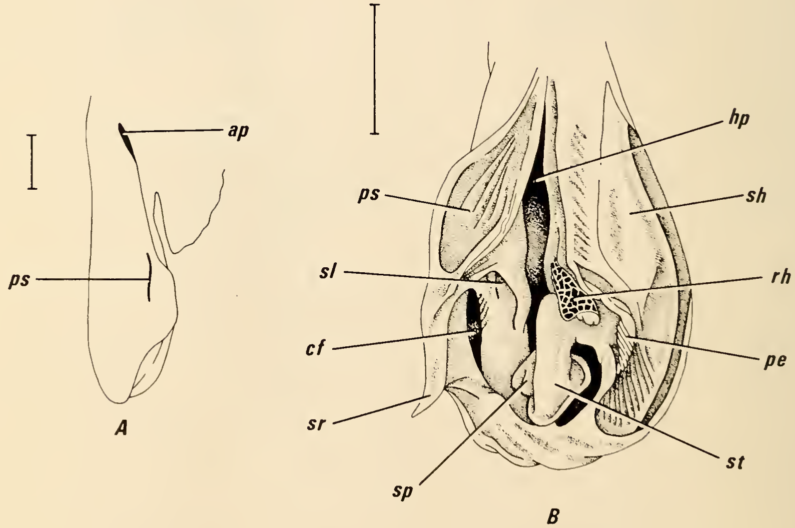

Fig. 6. *Raja radiata* (North Atlantic). A. external view of right clasper from dorsal side; B. lateral view of right clasper opened to show structural features of the glans. Scale 2,0 cm.
ap—apopyle; cf—cleft; hp—hypopyle; pe—pent; rh—rhipidion; ps—pseudosiphon; sl—slit; sh—shield; sp—spike; sr—spur; st—sentinel.

Raja clavata, *R. blanda* and others, Stehmann (1969, 1970) has referred to this structure as the 'inner pseudosiphon', but because it houses the sentinel in these species, Hulley (1970) has proposed the term pocket. This has been followed by Stehmann (1971*a*, *b*), who recognizes a pocket, rather than an inner pseudosiphon, in *Raja herwigi* and *R. maderensis*. However, it should be noted that the pseudosiphon which Leigh-Sharpe (1924) described in *Raja marginata* is entirely different to the pocket, and has been referred to the term cleft.

Stehmann (1969) expresses some concern as to the question of priority in terminology. However, an accurate definition for the pseudosiphon was never given, since Leigh-Sharpe (1920–6) made numerous misidentifications of this structure, presumably discriminating it by its position in the clasper alone. Ishiyama's definition can therefore be used (see p. 19).

It should be noted that Stehmann (1970) has distinguished a pseudosiphon in the species *Raja fyllae*. I have found that in this species, as in *Raja wallacei* (Fig. 7 A) and *R. caudaspinosa*, the cavity on the outer dorsal wall is formed by an indentation in the musculature which is attached to the dorsal terminal 1 (*m. dilatator*), and further that this cavity is not found in all specimens. I have therefore not described this as a real and separate structure, comparable to the pseudosiphon. Stehmann (personal communication) feels that this must be left to the discretion of the author.

In *Cruriraja* species, the dorsal terminal 1 is differently situated (Figs 40, 41, 42), so that it does not overlie the other dorsal terminal cartilages to any great

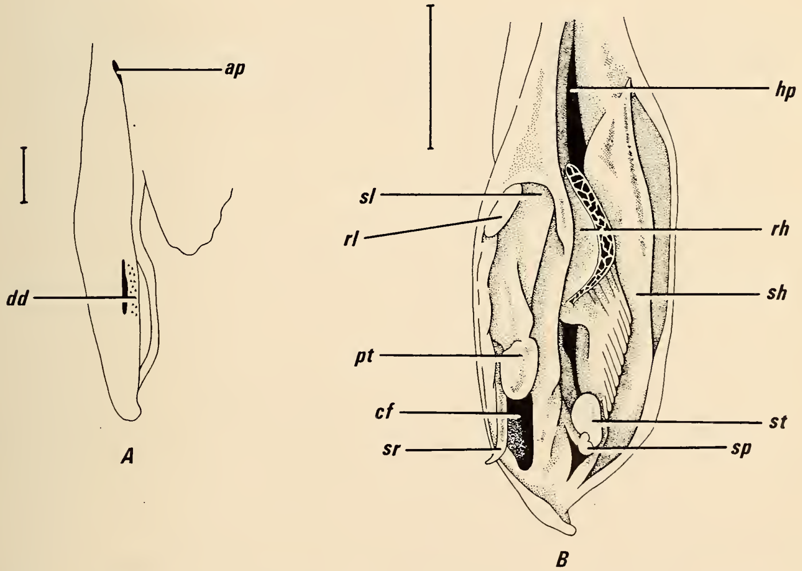

Fig. 7. *Raja wallacei*. A. external view of right clasper from dorsal side; B. lateral view of right clasper opened to show structural features of the glans. Scale 2,0 cm. ap—apopyle; cf—cleft; dd—dermal denticles; hp—hypopyle; pt—promontory; rh—rhipidion; rl—roll; sh—shield; sl—slit; sp—spike; sr—spur; st—sentinel.

extent. However, a small cavity is formed between the distal end of the dorsal terminal 2 and the concavity of the dorsal terminal 1. This cavity is situated on the inner surface of the dorsal lobe of the glans. Because of its close association with the dorsal terminal 1 cartilage, I have termed this structure the pseudosiphon, but it is obviously formed in a different manner and lies transversally to, rather than in the longitudinal axis of, the clasper. It may therefore necessitate the introduction of a new term.

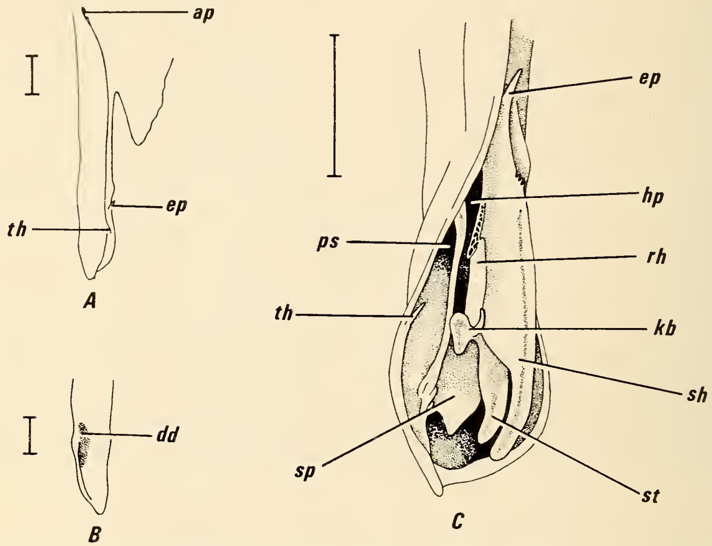

Fig. 8. *Cruriraja triangularis*. A. external view of right clasper from dorsal side. B. ventral surface of right clasper; C. lateral view of right clasper opened to show structural features of the glans. Scale 1,0 cm.
ap—apopyle; dd—dermal denticles; ep—eperon; hp—hypopyle; kb—knob; ps—pseudosiphon; rh—rhipidion; sh—shield; sp—spike; st—sentinel; th—thorn.

In some Batoidei (Figs 12 A–H), there is a cavity situated on the outer surface of the ventral lobe of the glans, which I have termed the ventral pseudosiphon, again because of its close association with the dorsal terminal 1 cartilage. This corresponds to the lateral pocket of Jungersen (1899). Leigh-Sharpe (1920–6) has termed this the slit (see below), sentina and crumena in *Torpedo marmorata*, *Rhinobatos productus* and *Cestracion philippi* respectively, but in others, *Trygon pastinacea* and *Myliobatis aquila*, has left it unlabelled. Similarly, Ishiyama (1958) does not label this structure in *Rhinobatos schlegeli* and *Platyrhina sinensis*.

(2) *slit*

Leigh-Sharpe (1920–6) does not clearly define the term slit, mentioning it only as a cavity, which may be internal, e.g. *Raja batis*, *R. lintea*, or may be situated on the outer surface of the dorsal lobe, e.g. *Raja murrayi*, *R. eatoni*. From its position in the latter species, and from the fact that *Raja eatoni* is considered to be synonymous with *Bathyraja smithii* (Hulley 1970), it may be concluded that these cavities correspond to pseudosiphons, according to the above proposed definition.

Ishiyama (1958: 202) defines the slit as a 'small, shallow cavity formed by fleshy skin on the inner surface of the dorsal lobe and has no relation to dorsal terminal 1'.

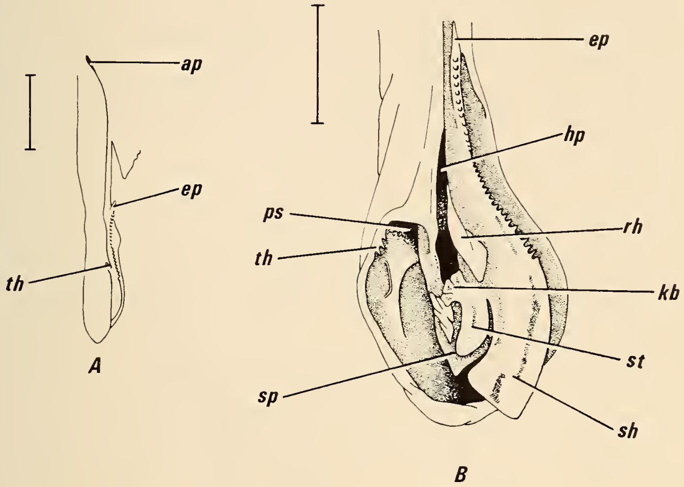

Fig. 9. *Cruriraja rugosa*. A. external view of right clasper from dorsal side. B. lateral view of right clasper opened to show structural features of the glans. Scale 2,0 cm. ap—apopyle; ep—eperon; hp—hypopyle; kb—knob; ps—pseudosiphon; rh—rhipidion; sh—shield; sp—spike; st—sentinel; th—thorn.

Stehmann (1969) points out that Ishiyama has not used the term consistently, especially where there are two or more cavities on the inner surface of the dorsal lobe. He recognizes that two structures (not including the pseudosiphon) may be involved: (1) a skinny flap, situated proximally in the glans, which has no relation to any dorsal terminal cartilage, and is so orientated that the sac lies at right angles to the longitudinal axis of the clasper; and (2) a cavity which may be formed between any dorsal terminal cartilage (other than the dorsal terminal 1) and the axial or dorsal marginal cartilage, i.e. it is a cavity which is bounded by cartilaginous elements. The first cavity is regarded as the slit, the second has been termed the cleft. I agree with this distinction, and have subsequently used Stehmann's definitions for these dorsal cavities.

It should be noted that the cavity formed in the ventral lobe of the clasper in Dasyatidae and Mobulidae, and which has been referred to as a slit by Leigh-Sharpe (1920: fig. 15; 1926: figs 12, 14, 15), is now referred to as a ventral pseudosiphon. The slit is therefore always situated on the inner surface of the dorsal lobe of the glans.

(3) *rhipidion: pseudorhipidion*

Definitions for both these structures have been given by Ishiyama (1958), who relates the smooth-surfaced, dorsally situated pseudorhipidion to the distal end of the dorsal marginal cartilage, while pointing out that the pitted, ventrally situated rhipidion is composed entirely of erectile tissue and has no relation to cartilaginous elements. Stehmann (1969), however, points out that Ishiyama is incorrect in his restriction of the term rhipidion to *Raja* species (1958) or *Raja* and *Breviraja* species (Ishiyama & Hubbs 1968), and pseudorhipidion to *Bathyraja*, since members of his *clavata*-group (subgenus *Raja*: Stehmann (1970)) possess a pseudorhipidion. The presence of a pseudorhipidion is therefore not a suitable character for the separation of the genus *Bathyraja* from other rajids.

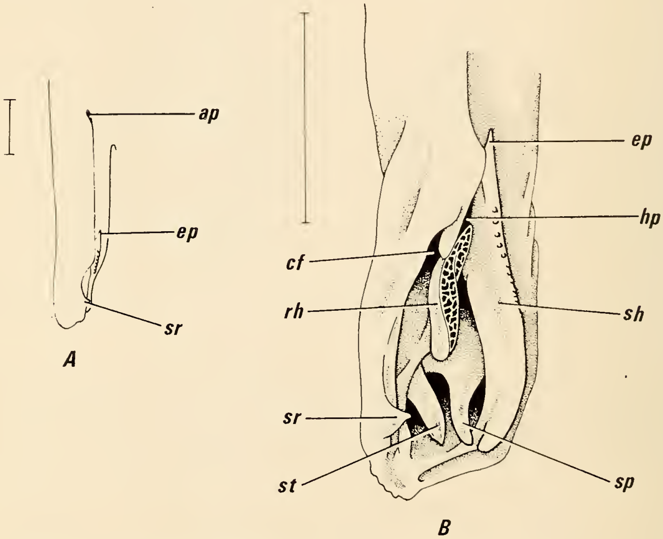

Fig. 10. *Anacanthobatis marmoratus*. A. external view of right clasper from dorsal side; B. lateral view of right clasper opened to show structural features of the glans. Scale 1,0 cm.
ap—apopyle; cf—cleft; ep—eperon; hp—hypopyle; rh—rhipidion; sh—shield; sp—spike; sr—spur; st—sentinel.

(4) *spur*

Leigh-Sharpe (1920–6) described this structure in *Raja radiata*, referring to it as a hard, cartilaginous point, which curves outward from the dorsal lobe of the glans (Fig. 6 B, *sr*). Stehmann (1969, 1970) has shown that this structure is directly related to the dorsal terminal 3 cartilage. On the other hand, Ishiyama (1958) refers the spur to a structure on the inner surface of the ventral lobe, which is formed by the accessory terminal, while Ishiyama & Hubbs (1968: figs 2 A, B) refer the spur to the ventral terminal cartilage. It is felt that Leigh-Sharpe and Stehmann should be followed, and that Ishiyama should redefine his structures.

(5) *funnel*

The term was introduced by Ishiyama (1958: 203) as 'a component located on the distal portion of the ventral lobe, having a soft projection like the foot of a bivalve mussel'. He relates this structure directly to the ventral terminal cartilage.

It can be seen that in those species in which the funnel is present (Ishiyama 1958: fig. 4) it always overlies the 'spur', where this is present, on the inner ventral surface. Examination of the corresponding cartilages (Ishiyama 1958: fig. 12) reveals that in these species the only cartilage which can possibly overlie the accessory terminal ('spur') is the distal end of the ventral marginal. Furthermore, Ishiyama (1958) introduces the term claw for the species *Rhinoraja odai* and *Rhinoraja longicauda*, relating this to a modification of the accessory terminal cartilage. However, he shows (1958: fig. 11) that the accessory terminal in these species is a single cartilage, which is flat and sharp-edged and quite unlike the external claw. Again, examination of the figures (Ishiyama 1958: fig. 12) shows that the cartilage which overlies the accessory terminal (knife), and is extended distally, is the ventral marginal cartilage.

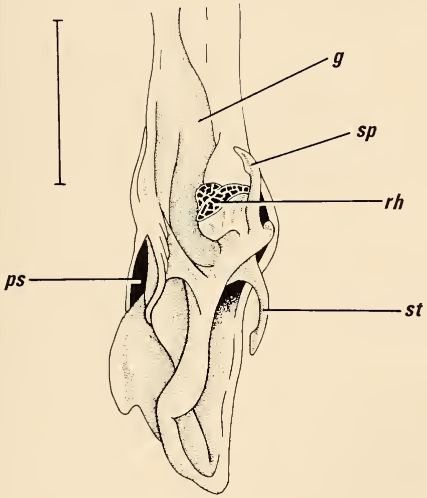

Fig. 11. *Anacanthobatis americanus*. Lateral view of right clasper opened to show structural features of the glans. Scale 1,0 cm.
g—clasper groove; ps—pseudosiphon; rh—rhipidion; sp—spike; st—sentinel.

This means therefore that neither the ventral terminal nor the accessory terminal can be related to the term funnel or claw, and that clearly the ventral marginal is the associated cartilage in both cases. Further confusion is added because the claw in *Rhinobatos schlegeli* and *Rhinobatos annulatus* (Ishiyama 1958: figs 13, 14) is formed by the accessory terminal cartilage.

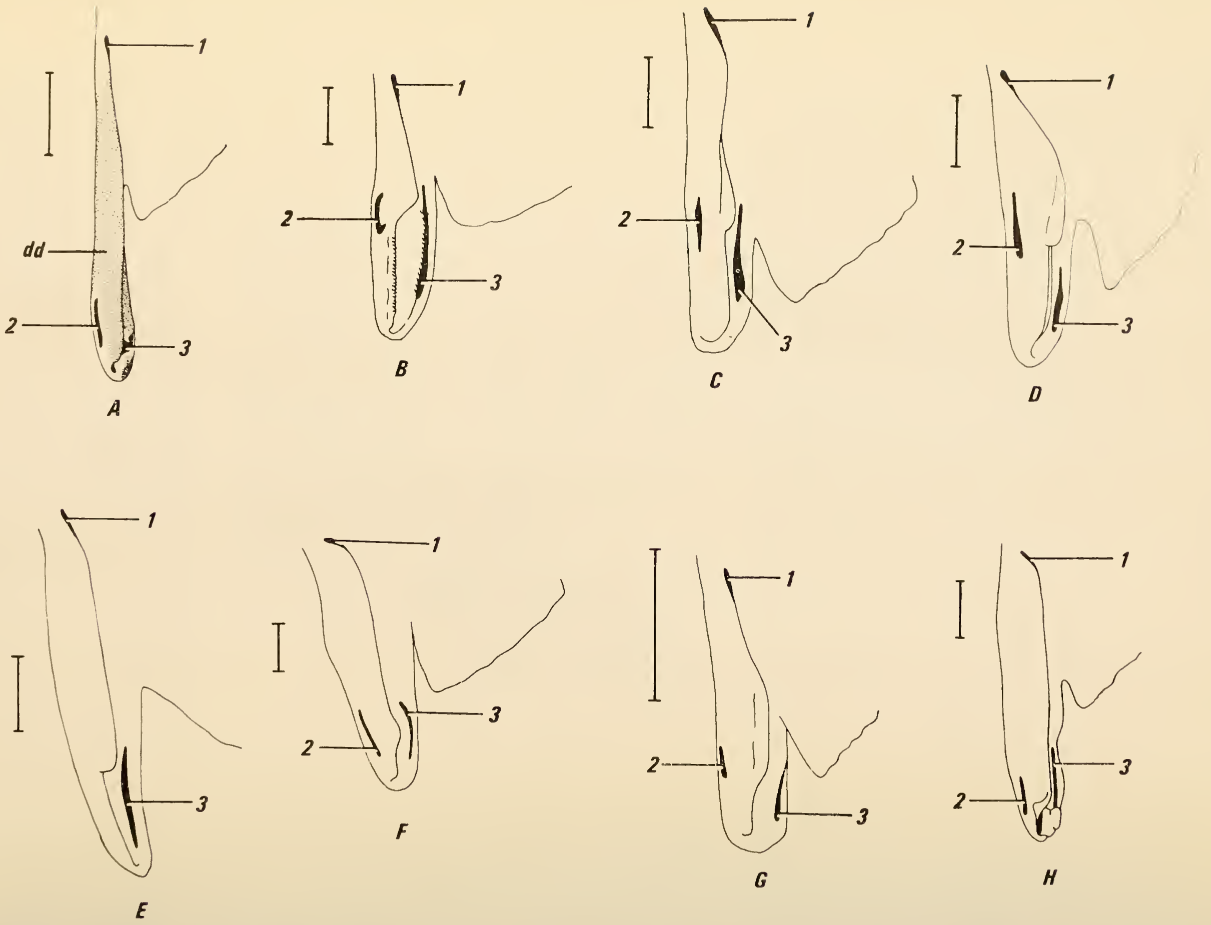

Fig. 12. External view of right clasper of southern African Batoidei (excluding Rajoidea) from dorsal side. 1—apopyle; 2—pseudosiphon; 3—ventral pseudosiphon; dd—dermal denticles. Scale 2,0 cm. A. *Rhinobatos ocellatus*; B. *Gymnura natalensis*; C. *Rhinoptera javanica*; D. *Mobula diabolus*; E. *Dasyatis thetidis*; F. *Urotrygon daviesi*; G. *Heteronarce garmani* (scale 1,0 cm); H. *Torpedo nobiliana*.

Stehmann (1969) correctly follows Ishiyama's definition, relating the term funnel to the ventral terminal cartilage, while introducing Leigh-Sharpe's term, projection, for the distally situated, elongate, cartilaginous structure formed by the ventral marginal cartilage. Hence the term projection of Stehmann (1969, 1970) is equivalent to the terms funnel/claw of Ishiyama, while the term funnel of Stehmann is clearly a different structure.

It should be noted that although Leigh-Sharpe (1926) did not include the term projection in his list of clasper components, and does not adequately define this structure, he shows that in *Raja lintea* (1924: fig. 6) the projection is an expansion on the inner lateral edge of the shield. This can therefore be related directly to the ventral terminal cartilage, and as such, is a different structure to the projection of Stehmann.

It is suggested that the term funnel be applied to the distal protrusion of the ventral terminal cartilage, as in *Raja clavata* (Fig. 22), while the structure which is related to the distal protrusion of the ventral marginal be known as the projection. The adoption of this convention would avoid further confusion, especially with regard to Stehmann's definitions.

The structure which is regarded as the projection by Leigh-Sharpe must therefore be referred to some other term, if in fact it is an identifiable and real clasper component.

Furthermore, the projection as now defined would cover the terms spike in *Raja murrayi* and the sentinel in *Raja eatoni* (Leigh-Sharpe 1924: figs 13, 14). The term claw should be retained and reserved solely for the structure formed by the accessory terminal cartilage in *Rhinobatos*, *Platyrhina* and *Myliobatis*.

(6) *pecten*

The structure was recognized as a component in *Raja marginata* (= *Raja alba*) and was defined (Leigh-Sharpe 1924) as a long, hard structure, bearing six or more hard projections or serrations, which is situated on the outer lateral margin of the dorsal lobe of the clasper.

Dissection of the clasper of *Raja alba* (Fig. 33) has revealed that the pecten is directly related to the sharp protuberances or serrations, which are developed on the outer lateral margin of the dorsal terminal 3 cartilage. A pecten was also described in the clasper of *Raja miraletus* (Hulley 1969), but in this species the dorsal terminal 2 cartilage is involved. However, since the serrations are developed in a similar position to those in *Raja alba*, and since the orientation and probably the function is identical, I have termed both structures the pecten. This has been followed by Stehmann (1971*a*), who distinguishes a pecten, formed by the dorsal terminal 2 cartilage, in *Raja herwigi*.

(7) *scale and dermal denticles*

Ishiyama (1958) pointed out that in two Japanese subspecies, *Bathyraja smirnovi smirnovi* and *B. smirnovi ankasube*, minute scales were present on the outer border of the ridge. As such a phenomenon had not been reported for

European rajids, he recognized them as a separate clasper component, which he defined as the scale.

Dermal denticles are present on the outer surface of the dorsal lobe of the claspers of *Raja confundens*, *R. leopardus* and *R. wallacei* (Hulley 1970: figs 17–19). Although the lateral area would correspond with the ridge, if this had been developed, I have preferred to regard such denticles as a separate component to Ishiyama's scale.

This means, therefore, that scale is a term which is restricted to dermal denticles on the ridge, and is probably only applicable in the genus *Bathyraja*, in which the ridge is developed. Dermal denticles are found in other rajid genera. However, both these components have a similar derivation and as such could possibly be referred to the same term.

(8) *terminal bridge*

Ishiyama (1958) first described the terminal bridge as a short, bar-like cartilage, which connects the axial cartilage with the distal end of the dorsal terminal 2 cartilage. He derived the terminal bridge from an offshoot of the accessory terminal 2. However, he does not recognize this as a separate clasper component (1958: tables 3, 4). Hulley (1966, 1969) also recognized the existence of this linking cartilage in *Raja pullopunctata*, where it separates the two dorsal clefts, and in *Raja miraletus*, where it separates the cleft from the pocket. In both species, the terminal bridge links the axial with the dorsal terminal 2 cartilage.

Stehmann (1969, 1970, 1971*a*, *b*) regards the terminal bridge as a real component, identifiable in the external anatomy of the claspers of *Raja brachyura*, *R. montagui*, *R. herwigi*, *R. maderensis* and *R. straeleni*, and directly related to the development of one or two small, cartilaginous rods. In these species, the rods link the axial with the dorsal terminal 2 cartilage and separate the cleft from the pocket.

I have found this linking cartilage in *Raja doutrei*, where it joins the axial to the dorsal terminal 2 (Fig. 30), thereby separating the two clefts in the dorsal lobe. It is absent in *Raja lanceorostrata* (Fig. 31), where the dorsal terminal 2 itself makes contact with the axial. This is the case with *Raja radiata*, *R. dissimilis*, *R. caudaspinosa*, *R. confundens* and *R. leopardus*, but in *R. wallacei* the connection is formed between the axial and the dorsal terminal 3 cartilage.

Furthermore, a cartilaginous connection is present in *Cruriraja parcomaculata*, *C. triangularis* and *C. rugosa* (Figs 40–42), but in these species the connection is completely different from the above. It is made between the accessory terminal 2 and the axial. It would appear, therefore, that the terminal bridge is not constant in orientation and it is suggested that this element helps bind the cartilages of the terminal group to the axial, thereby acting antagonistically to the contraction of the *m. dilatator*.

Because of this, and because of the different areas of insertion (dorsal terminal 2, accessory terminal 2), it is felt that the terminal bridge should not be recognized as a separate and distinct component, even though it might be evident in the external and internal morphology of the glans (cf. Stehmann 1971*b*).

(9) *pent*

The term was originally used to describe a ventral, ridge-like fold in *Trygon pastinacea* (Leigh-Sharpe 1922: fig. 17). This fold is situated at about the level of the hypopyle and presumably acts in much the same way as the rhipidion. Ishiyama (1958: fig. 4 A) recognizes a pent in *Bathyraja tobitukai*, which is similarly positioned in the glans.

The pent described by Stehmann (1969, 1970) is an elongate ridge, which is pleated and runs parallel to the midline of the organ, from the distal end of the rhipidion. Although this does not appear to be equivalent to the above, Stehmann's definition has been followed to avoid further confusion.

(10) *sentina*

The sentina originally described by Leigh-Sharpe (1922) was an external cavity in *Rhinobatos productus*. This cavity was subsequently labelled as the slit or crumena in later papers by this author. As has been pointed out above, the external cavity on the ventral surface of the clasper has now been termed the ventral pseudosiphon, because of its association with the dorsal terminal 1 cartilage. The term sentina has been reserved for an internal structure of the glans, and is defined below.

(11) *promontory*

The promontory recognized by Ishiyama & Hubbs (1968: figs 2 C, D) in *Breviraja colesi* is clearly related to the proximal region of the dorsal terminal 3 cartilage. On this basis, the promontory was recognized in *Raja wallacei* (Hulley 1970: fig. 19). However, Leigh-Sharpe (1920–6) and Stehmann (1969, 1970) regard the promontory as the distal projection of the dorsal terminal 2 cartilage, while the structure associated with the dorsal terminal 3 is termed the roll. This interpretation is accepted and to avoid confusion the structures have been reidentified and relabelled in *Raja wallacei* (Fig. 7).

Description

Definitions of the external components of the clasper glans of southern African Rajoidea are given below, and their occurrence is described and figured (Figs 5–14; Hulley 1970: figs 4–21). For definitions of the apopyle and siphon gland, the reader should refer to Leigh-Sharpe (1920–6).

Components of the dorsal lobe

(1) *pseudosiphon* (Ishiyama)

A cavity situated on the outer surface of the dorsal lobe of the glans at about the level of the hypopyle; it has an oval aperture, the long axis of which is orientated in the longitudinal axis of the organ; its degree of development is directly dependent upon the shape and location of the dorsal terminal 1 cartilage.

A pseudosiphon is present in *Bathyraja smithii* (Hulley 1970: fig. 21), *Raja robertsi* (Hulley 1970: fig. 12) and *R. radiata* (Fig. 6) where it is situated on the outer surface of the dorsal lobe. In these species, the outer lateral margin of the pseudosiphon is formed by the dorsal terminal 1 cartilage, so that the cavity can be easily seen and opened by spreading this cartilage. A groove, which is similarly located, is found in some specimens of *Raja caudaspinosa* and *R. wallacei* (Fig. 7), but since this is developed as a fold in the musculature, and is not present in all specimens, it has not been identified as the pseudosiphon (cf. *Raja fyllae*, *R. fullonica*: Stehmann 1969; 1970).

In *Cruriraja* species (Hulley 1970: fig. 4; Figs 8, 9) a pseudosiphon has been distinguished on the inner surface of the dorsal lobe. Unlike the above, this cavity has a transverse aperture, but since it has a relationship with the dorsal terminal 1 cartilage, it has been termed the pseudosiphon.

The outer lateral edge of the dorsal terminal 1 also forms the dorsal lip of the pseudosiphon in *Anacanthobatis americanus* (Fig. 11), which, unlike the South African species *A. marmoratus*, possesses a pseudosiphon on the outer dorsal wall of the glans.

Both *Rhinobatos annulatus* (Fig. 13) and *Myliobatis cervus* (Fig. 14) possess a pseudosiphon in the outer dorsal wall. However, it should be noted that in these species, as in *Rhinobatos schlegeli* and *Platyrhina sinensis* (Ishiyama 1958), the dorsal terminal 1 is situated on the ventral side of the glans.

A brief examination of the following southern African Batoidei has confirmed the presence of a pseudosiphon in *Rhinobatos ocellatus*, *Gymnura*

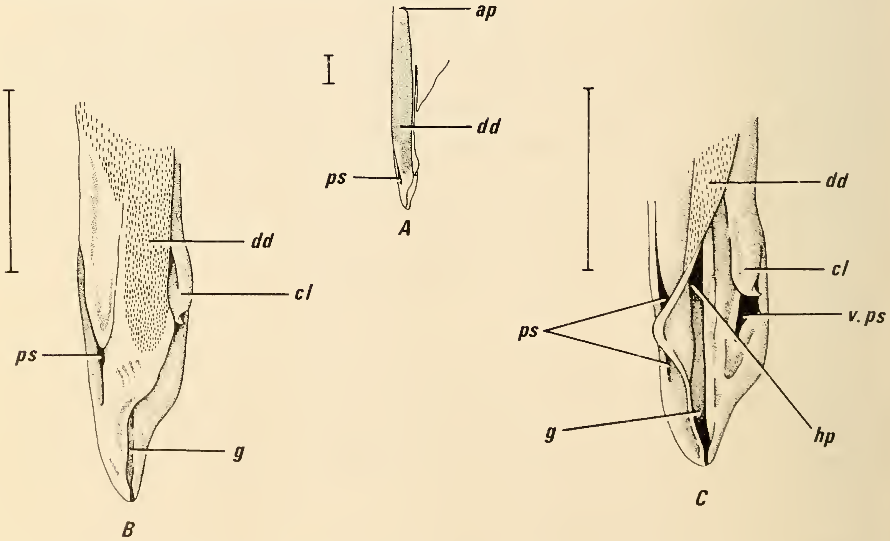

Fig. 13. *Rhinobatos annulatus*. A. external view of right clasper from dorsal side; B. distal tip of right clasper; C. lateral view of right clasper opened to show structural features of the glans. Scale 1,0 cm.
ap—apopyle; cl—claw; dd—dermal denticles; g—clasper groove; hp—hypopyle; ps—pseudosiphon; v.ps—ventral pseudosiphon.

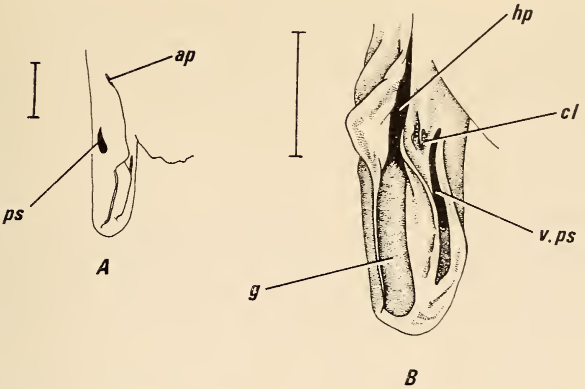

Fig. 14. *Myliobatis cervus*. A. external view of right clasper from dorsal side; B. lateral view of right clasper opened to show structural features of glans. Scale 2,0 cm.
ap—apopyle; cl—claw; g—clasper groove; hp—hypopyle; ps—pseudosiphon; v.ps—ventral pseudosiphon.

natalensis, *Mobula diabolus*, *Rhinoptera javanica*, *Heteronarce garmani* and *Torpedo nobiliana* (Fig. 12). The pseudosiphon in these species is dorsally situated and should not be confused with the cavity on the ventral surface, which has been identified as the ventral pseudosiphon (Fig. 12).

(2) *cleft* (Stehmann)

A small cavity, situated on the inner surface of the dorsal lobe of the glans, which is formed between the axial or dorsal marginal cartilages and any other dorsal terminal cartilage except the dorsal terminal 1, i.e. a cavity bounded by cartilages other than the dorsal terminal 1 cartilage.

Two clefts are present in *Raja doutrei*, *R. pullopunctata*, *R. lanceorostrata*, *R. caudaspinosa* and *R. dissimilis* (Hulley 1970: figs 5, 6, 7, 15; Fig. 5). The proximal cleft in these species is formed as a cavity between the axial cartilage and the dorsal terminal 2. A similar gap between these cartilages is found in *Raja wallacei*, *R. confundens* and *R. leopardus* (Figs 35–37), but a proximal cleft is not present externally. In *Raja confundens* and *R. leopardus* the axial and dorsal terminal 2 are in close proximity, while in *Raja wallacei* the gap is closed by the protrusion of the promontory (dorsal terminal 2). A slit is developed in this region in the species.

The cleft in the species *Raja clavata*, *R. straeleni*, *R. alba* and *R. miraletus* (Hulley 1970: figs 8–11) is differently formed, in that the cartilages bounding the cavity are the dorsal marginal and the dorsal terminal 2.

A distal cleft occurs in all species except *Raja alba*, *R. clavata*, *R. straeleni* and *R. miraletus*; in *R. pullopunctata* (Hulley 1966: fig. 5) the distal cleft is formed between the axial cartilage and the dorsal terminal 2; in *R. doutrei* and *R. lanceorostrata* (Figs 30, 31) between the axial and dorsal terminal 3; and in *R. radiata*, *R. caudaspinosa*, *R. dissimilis*, *R. wallacei*, *R. confundens* and *R. leopardus* between the axial and dorsal terminal 4 (Figs 34–39). It is interesting to note that when a distal cleft is present, the proximal border of this cleft is always formed either by the terminal bridge or the dorsal terminal 2 cartilage.

While a proximally situated cleft is present in *Anacanthobatis marmoratus* (Fig. 10), it is absent in *A. americanus*. A cleft is also absent in *Bathyraja smithii* and *Rhinobatos annulatus*.

(3) *slit* (Leigh-Sharpe)

A small, blindly-ending sac, formed as a skinny flap on the inner dorsal surface of the proximal region of the glans; it is not bordered by cartilaginous elements and is not associated with cartilages. Two or more slits may be developed (Ishiyama 1958; 1967).

This structure is present in *Raja radiata*, *R. leopardus*, *R. wallacei*, *R. confundens* and *Bathyraja smithii* (Figs 6, 7; Hulley 1970: figs 17–19, 21). In these, the gap formed between the axial cartilage and the dorsal terminal 2 appears to be obscured by the development of other cartilages in this area, i.e. in *Raja radiata* by the dorsal marginal (Fig. 34), in *R. wallacei* by the dorsal terminal 2 (Fig. 35) and in *R. confundens* and *R. leopardus* by the close proximity of the dorsal terminal 2 cartilage to the axial (Figs 36, 37).

(4) *pocket* (new term)

A small, shallow cavity, which is situated distally on the inner dorsal wall of the clasper glans; it is bordered medially by the axial cartilage, while its outer lateral wall consists of connective tissue, which runs between the dorsal terminal 2 and the axial tip. It serves as a covering for the sentinel, in those species in which the sentinel is massively developed.

A pocket is present in *Raja clavata*, *R. straeleni* and *R. miraletus* (Hulley 1970: figs 9–11) and has been recognized in *R. herwigi* and *R. maderensis* (Stehmann 1971*a*, *b*).

(5) *pseudorhipidion* (Ishiyama)

A cartilaginous tongue, situated on the inner lateral margin of the dorsal lobe of the glans, close to the midline and at about the level of the hypopyle; it is formed by the distal projection of the dorsal marginal cartilage into the glans. Its function is to spread the ejaculating spermatozoa (Leigh-Sharpe 1920).

A pseudorhipidion is present in *Raja clavata*, *R. straeleni* and *R. miraletus* (Hulley 1970: figs 9–11), where it runs parallel to the midline of the organ for about one-third the length of the glans. However, in *Raja alba* (Hulley 1970: fig. 8) the pseudorhipidion is slightly twisted and extends for almost half the length of the glans; it is divisible into two areas: proximally the dorsal marginal is covered by loose, fleshy skin, but distally the integument becomes tightly bonded to the cartilage, so that the median, expanded region of the pseudorhipidion is exposed as a sharp cartilage.

Although Ishiyama (1958) distinguishes a pseudorhipidion in several Japanese rajids and restricts its occurrence to the genus *Bathyraja* (Ishiyama & Hubbs 1968), a pseudorhipidion has not been distinguished in the South African *Bathyraja smithii*. It should be noted, however, that in this species the dorsal marginal cartilage extends well into the clasper glans and has a raised lip on its outer lateral margin (Fig. 29); this would correspond to the pseudorhipidion, if it were developed externally.

(6) *pecten* (Leigh-Sharpe)

A cartilaginous structure located on the outer lateral margin of the dorsal lobe of the glans, at about the level of the hypopyle; it consists of six or more sharp, comb-like processes and is associated with the degree of development of the dorsal terminal 2 or dorsal terminal 3 cartilage.

The pecten is present in *Raja alba* and *R. miraletus* (Hulley 1970: figs 8, 9, *cm*). In *Raja straeleni*, the dorsal terminal 2 (Fig. 18 g) bears a number o small, blunt protuberances, corresponding in position to the pecten. These do not penetrate the integument of the outer wall of the clasper, and therefore do not manifest themselves as a pecten in this species. Stehmann (1971*a*) recognizes a pecten in *Raja herwigi*, which is formed in the same way as in *R. miraletus*.

(7) *dermal denticles* (new term)

Dermal denticles may be present on the outer border of the dorsal lobe of the clasper, where they may be close-set or widely separated.

Dermal denticles are present in *Rhinobatos annulatus*, *Raja confundens*, *R. leopardus* and *R. wallacei* (Figs 7, 13; Hulley 1970: figs 17–19) on the outer surface of the dorsal lobe. In *Cruriraja triangularis* (Fig. 8) they are developed on the ventral lobe of the glans. The term dermal denticles is discussed above in relation to the term scale.

(8) *ridge* (Ishiyama)

The ridge is the thickened and somewhat raised outer lateral border of the dorsal lobe; it extends from about the level of the hypopyle almost to the distal end of the clasper; it is directly related to the degree of development of the outer lateral edge of the dorsal terminal 2 cartilage.

The ridge is present in a single species only, *Bathyraja smithii* (Hulley 1970: fig. 21), in which it appears to be somewhat pleated and does not develop scale.

(9) *spur* (Leigh-Sharpe)

A hard, cartilaginous element, arising on the outer lateral margin of the dorsal lobe at about the level of the rhipidion, and curving outwards; it is formed by the dorsal terminal 3 cartilage, which appears to be movable, so that when the clasper glans is opened it protrudes from the outer lateral margin.

A spur is present in *Raja radiata*, *R. wallacei* and *Anacanthobatis marmoratus* (Figs 6, 7, 10). Although the sharp point of the dorsal terminal 3 cartilage did not protrude through the integument of the outer wall of the cleft in the type of *Raja wallacei* (Hulley 1970: fig. 19), examination of the cartilages revealed the hooked dorsal terminal 3 cartilage. Further material of this species, which has only just come to hand, confirms the presence of the spur (Fig. 7).

(10) *thorn* (new term)

A structure consisting or one or more small, sharp points, situated on the outer lateral margin of the dorsal lobe, at about the level of the hypopyle; it is formed directly from processes developed on the proximo-lateral edge of the dorsal terminal 1 cartilage.

A thorn has been found in *Cruriraja parcomaculata*, *C. triangularis* and *C. rugosa* (Figs 8, 9; Hulley 1970: fig. 4).

(11) *promontory* (Leigh-Sharpe)

A cartilaginous element situated at the proximal end of the cleft; it consists of a cartilaginous tongue, which is more or less covered by a thick layer of integument; it is formed by the distal projection of the dorsal terminal 2 cartilage.

A promontory has been found only in *Raja wallacei* (Fig. 7), where it arises at the medial region of the dorsal lobe and projects into the cleft.

(12) *roll* (Stehmann)

A fleshy structure situated in the proximo-lateral region of the dorsal lobe and orientated to run parallel to the outer margin; it is associated with the promontory and probably arises as a fleshy expansion of the proximal end of the dorsal terminal 3 cartilage.

A roll has been found only in *Raja wallacei* (Fig. 7).

Components of the ventral lobe

It should be noted that while certain structures are developed on the outer surface of the dorsal lobe (pseudosiphon, pecten, dermal denticles), no components are developed on the outer surface of the ventral lobe in Rajoidea, except for dermal denticles in *Cruriraja triangularis* (Fig. 8 B). However, in some Batoidei a blindly ending cavity, which has been termed the ventral pseudosiphon, because of its relation with the dorsal terminal 1 cartilage, is present (Fig. 12). The following structures are therefore all found within the glans:

(1) *shield* (Leigh-Sharpe)

An elongate, plate-like structure, extending along the outer lateral edge of the ventral lobe, from about the level of the hypopyle; it may be dorsally convex and covered by pleated epithelia, except along its outer lateral margin, which is sharp-edged; it is directly associated with the degree of development of the outer lateral margin of the ventral terminal cartilage.

With the exception of *Bathyraja smithii* (Hulley 1970: fig. 21) and *Anacanthobatis americanus* (Fig. 11), a shield is present in all the examined rajoids. However, it was found to be absent in other Batoidei.

In the majority of rajids, the shield extends from about the level of the hypopyle to the distal tip of the clasper, and may be covered entirely by pleated epithelia, e.g. *Raja doutrei*, *R. lanceorostrata*, *R. alba*, *R. miraletus* (Hulley 1970: figs 5, 8, 9; Fig. 5) or covered only on its distal half with pleated epithelia, e.g. *Cruriraja parcomaculata*, *C. triangularis*, *C. rugosa*, *Raja caudaspinosa*, *R. confundens*, *Anacanthobatis marmoratus* (Figs 8, 9, 10; Hulley 1970: figs 4, 7, 17). In *Raja clavata* (Hulley 1970: fig. 10), unlike in *R. straeleni* (Hulley 1970: fig. 11), the shield is not well developed.

(2) *rhipidion* (Ishiyama)

An elongate, fan-shaped structure, consisting of porous, erectile tissue, which is situated on the inner border of the ventral lobe, and extends in the longitudinal axis of the clasper, from about the level of the hypopyle to about half the length of the glans; it is not associated with any cartilaginous element.

The rhipidion is elongate and free in *Raja doutrei*, *R. lanceorostrata*, *R. pullopunctata*, *R. caudaspinosa*, *R. radiata*, *R. dissimilis*, *R. confundens*, *R. leopardus*, *R. wallacei*, *Anacanthobatis americanus* and *A. marmoratus* (Figs 5, 6, 10, 11; Hulley 1970: figs 5–7, 15, 17–19), but is small, triangular and fixed in *Cruriraja parcomaculata*, *C. triangularis* and *C. rugosa* (Figs 8, 9; Hulley 1970: fig. 4).

(3) *boss* (new term)

> A small, flattened, cartilaginous process, which is situated just below the rhipidion, and more medially than the knob; it is directly related to the development of a recurved lateral process of the accessory terminal 2 cartilage.

The boss has been found in a single species only, *Cruriraja parcomaculata* (Hulley 1970: fig. 4). Although a small process is developed on the accessory terminal 2 cartilage in both *Cruriraja rugosa* and *C. triangularis* (Fig. 27), the corresponding boss is not present as an external structure in the glans (Figs 8, 9).

(4) *knob* (new term)

> A process, or processes, situated medially to the shield at about one-half the length of the clasper glans; it consists of a number of flattened processes (usually 4), or a single, plate-like cartilaginous element, from which a laterally directed, sharp, recurved point arises; the knob is related to the development of processes on the medio-dorsal side of the accessory terminal 1 cartilage.

The knob was so called to describe the blunt protuberances found in *Cruriraja parcomaculata* (Hulley 1970: fig. 4), but is now defined so as to include the plate and laterally projecting point in *C. triangularis* (Fig. 8) and the single, flattened process in *C. rugosa* (Fig. 9).

(5) *eperon* (Leigh-Sharpe)

> A sharp, anteriorly directed, spur-like structure, which is situated proximally to the level of the hypopyle on the outer lateral margin of the clasper; it is an anterior projection of the ventral terminal cartilage and may be interpreted as the sharp apex of the shield.

An eperon is found in *Cruriraja parcomaculata*, *C. rugosa* and *Anacanthobatis marmoratus* (Figs 9, 10; Hulley 1970: fig. 4) and although Hulley (1970) pointed out that it is absent in *Cruriraja triangularis*, examination of further material has revealed that the eperon is present in this species.

In *Cruriraja triangularis*, *C. rugosa* and *Anacanthobatis marmoratus*, the eperon appears to be associated with the development of small processes or sharp serrations on the outer lateral edge of the shield. However, in *Cruriraja parcomaculata* the shield is smooth-edged.

The structure was first described by Leigh-Sharpe (1924) to cover a process in two South American species, *Raja cyclophora* and *R. platana*.

(6) *spike* (Leigh-Sharpe)

> A cartilaginous element of varying size and shape, which is covered by integument and is located in the distal region of the glans; it is formed by the distal tip of the accessory terminal 2 cartilage.

A spike was found to be present in all the species of Rajoidea examined, except *Raja alba* and *Bathyraja smithii*, and was found to be absent in the Rhinobatidae and Myliobatoidea.

In *Cruriraja parcomaculata*, *C. triangularis* and *C. rugosa* (Figs 8, 9; Hulley 1970: fig. 4), the spike resembles a flattened, leaf-like tongue, which is situated on the median axis of the clasper. In *Raja doutrei* and *R. pullopunctata* (Hulley 1970: figs 5, 6) the spike is also medially placed, but is sharp-pointed and straight, while in *R. lanceorostrata* (Fig. 5) it is hooked. The sentinel obscures the spike in *R. miraletus* and *R. radiata*. The spike in *R. miraletus* is somewhat sharp-pointed, but in *R. radiata* it is more or less bilobed. A bulbous, bilobed spike is found in *R. confundens* (Hulley 1970: fig. 17), while in *R. wallacei* (Fig. 7) the spike is bilobed and elongate. A simple, bulbous spike, which in some cases appears to arise from the dorsal lobe of the glans, is found in *R. caudaspinosa*, *R. dissimilis* and *R. leopardus* (Hulley 1970: figs 7, 15, 18). A distally situated, sharp-pointed spike, forming a border to the sentina is found in *R. straeleni* and *R. clavata* (Hulley 1970: figs 10, 11). *Anacanthobatis marmoratus* and *A. americanus* (Figs 10, 11) possess a somewhat similarly shaped spike, which in *A. americanus* is directed laterally outward.

(7) *sentinel* (Leigh-Sharpe)

A cartilaginous structure, varying considerably in shape and size and which may or may not be covered by fleshy integument, located on the midline of the clasper; it is formed by the distal region of the accessory terminal 1 cartilage.

This structure is present in all species of Rajoidea except *Bathyraja smithii* and *Raja pullopunctata* and in Rhinobatidae and Myliobatoidea. It should be noted that the terms knife and claw, which are also developed from the accessory terminal, when only one accessory terminal cartilage is present, are used for *Bathyraja smithii*, Rhinobatidae and Myliobatoidea (cf. Stehmann, 1970).

The sentinel in the genus *Cruriraja* (Figs 8, 9; Hulley 1970: fig. 4) is a flattened, spatulate, cartilaginous structure, which is situated medially to the shield. An enlarged sentinel, with a sharp, knife-like, outer lateral edge is found in *Raja clavata* and *R. straeleni* (Hulley 1970: figs 10, 11); an enlarged, but spade-shape sentinel is found in *R. miraletus* (Hulley 1970: fig. 9); a curved, dorsally convex sentinel is found in *R. radiata* (Fig. 6); and an enlarged, elongate sentinel is found in *R. alba* (Hulley 1970: fig. 8), where it extends to the distal tip of the glans.

Raja doutrei and *R. pullopunctata* (Fig. 5; Hulley 1970: fig. 5) possess small, knob-like sentinels; in *R. dissimilis*, *R. confundens* and *R. leopardus* (Hulley 1970: figs 15, 17, 18) the sentinel is foot-like and may protrude laterally from the median axis of the glans; the sentinel in *R. wallacei* (Fig. 7) is bulbous, while in *R. caudaspinosa* (Hulley 1970: fig. 7) it is small and dorso-ventrally flattened.

The sentinel in *Anacanthobatis marmoratus* (Fig. 10) is tongue-like and quite dissimilar to the spike, but in *A. americanus* (Fig. 11) the sentinel resembles the spike, although it points laterally inward.

(8) *signal* (Leigh-Sharpe)

A fleshy pad, which is located posterior to the hypopyle at about the same level as the pseudorhipidion, and which can rotate about the longitudinal axis of the clasper; it is formed by the accessory terminal 3 and accessory terminal 4 cartilages.

The structure is present in *Raja clavata* and *R. straeleni* (Hulley 1970: figs 10, 11), where it is formed by both the accessory terminal 3 and 4 cartilages. It can rotate so as to protrude from the opened glans. In *Raja miraletus* (Hulley 1970: fig. 9) the signal is formed from a single cartilage only, the accessory terminal 3, and does not appear to be movable.

(9) *knife* (Ishiyama)

A movable, cartilaginous structure with an axe shape, which is covered by integument at its base, but exposed along its 'cutting' edge; it is situated in the distal region of the ventral lobe and is usually partly obscured by the projection; it is formed by the accessory terminal 1 cartilage.

A knife is present in a single species only, *Bathyraja smithii* (Hulley 1970: fig. 21), in which it is almost entirely obscured from view by the well-developed projection.

(10) *funnel* (Stehmann)

A bluntly-rounded, cartilaginous tongue, resembling the foot of a bivalve mollusc, which is situated at the distal region of the ventral lobe of the clasper, so as to extend beyond the cavity of the glans, when this is opened; it is formed by the elongate, distal end of the ventral terminal cartilage.

The funnel is found in the species *Raja clavata* and *R. straeleni* (Hulley 1970: figs 10, 11). Ishiyama (1958) is of the opinion that this structure is present in the Japanese genera *Bathyraja* and *Rhinoraja*, but this is incorrect (see discussion on terminology).

(11) *projection* (Stehmann)

An elongate, finger-like, cartilaginous rod, which is covered by integument and which projects from the ventral lobe; it is formed by the distal elongation of the ventral marginal cartilage.

A projection has been recognized in *Bathyraja smithii* (Hulley 1970: fig. 21), where it projects laterally inwards and obscures the underlying knife from view. It is thickly covered by integument, so as to resemble the funnel, but may easily be distinguished from that structure (see above).

(12) *sentina* (Leigh-Sharpe)

A blindly ending sac, whose aperture points posteriorly, and which is located at the distal end of the clasper; it may be associated with the distal tip of the accessory terminal 2 cartilage.

A sentina is present in *Cruriraja parcomaculata*, *Raja caudaspinosa*, *R. miraletus*, *R. clavata*, *R. straeleni*, *R. confundens* and *R. wallacei* (Hulley 1970: figs 4, 7, 9–11, 17, 19). It is not easily identifiable, and should not be confused with the ventral pseudosiphon.

(13) *claw* (Ishiyama)

A small, sharp, cartilaginous point, which is situated on the ventral lobe at about the level of the hypopyle; it is formed by the accessory terminal 1 cartilage and is usually associated with a ventral pseudosiphon.

Among the species which have been examined in detail, a claw has been found only in *Rhinobatos annulatus* and *Myliobatis cervus* (Figs 13, 14), but it may well be present in other Rhinobatoidea and Myliobatoidea, e.g. *Rhinobatos ocellatus* (Fig. 12), *Rhinobatos schlegeli, Platyrhina sinensis* (Ishiyama 1958: fig. 20).

(14) *pent* (Leigh-Sharpe/Stehmann)

> An elongate ridge, which is covered by pleated integument and runs from the distal end of the rhipidion, parallel with the mid-line of the clasper; it is a fleshy structure, which is associated with the inner lateral edge of the ventral terminal cartilage.

A pent has been recognized in *Raja dissimilis, R. confundens, R. wallacei* and *R. radiata* (Figs 6, 7; Hulley 1970: figs 15, 17 (not labelled)), and may also be present in *R. caudaspinosa* and *R. leopardus.*

The skeleton of the clasper is a continuation, in the median axis, of the basipterygium, and is composed of three groups of cartilages, the basal group (including the basipterygium), the axial group and the terminal group.

Basal group

The basal group consists of three types of cartilages (Fig. 15): the basipterygium (B), the Beta-cartilage and a varying number of intermediate proximal segments (b_1–b_3). Ishiyama (1958) has pointed out that the basal group is not species specific, and although the number of proximal segments may vary within large groups of elasmobranchs (Huber 1901), the basal group may only be used in the interpretation of phylogenetic relationships (White 1937).

Huber (1901) pointed out that in the Platosomeae (Batoidei) the number of proximal segments varies between two and four. Ishiyama (1958) found that there are four intermediate segments in Platyrhinidae (*Platyrhina sinensis*), three in Rhinobatidae (*Rhinobatos schlegeli*), and only two in *Raja, Bathyraja* and *Rhinoraja* among the Rajidae, and on this basis has postulated that the Rhinobatidae are intermediate between the Platyrhinidae and the Rajidae. Some criticism of this theory may be raised by the fact that Jungersen (1899) and Huber (1901) recorded four intermediate segments in *Rhinobatos columnae*, but the present investigation supports Ishiyama, in that only three intermediate cartilages are present in *Rhinobatos annulatus* (Fig. 15 a) and *Rhinobatos ocellatus.*

This investigation of the basal group of cartilages, while including *Raja* and *Bathyraja*, has been expanded to incorporate the genus *Cruriraja* of the family Rajidae and *Anacanthobatis* of the family Anacanthobatidae, so that an overall picture of the basal group in the Rajoidea may be obtained.

It appears that in the Rajoidea (Fig. 15), the basipterygium is connected to the axial cartilage by two intermediate segments (b_1–b_2), which are partially covered dorsally by a flat, plate-like Beta-cartilage, serving as an area of attachment for the *m. flexor internus* (Jungersen 1899; Hulley 1966). Unlike the Rhinobatidae, the Beta-cartilage in the Rajoidea does not extend on to the axial cartilage, but terminates above the junction of the b_2—and axial cartilages (Fig. 15).

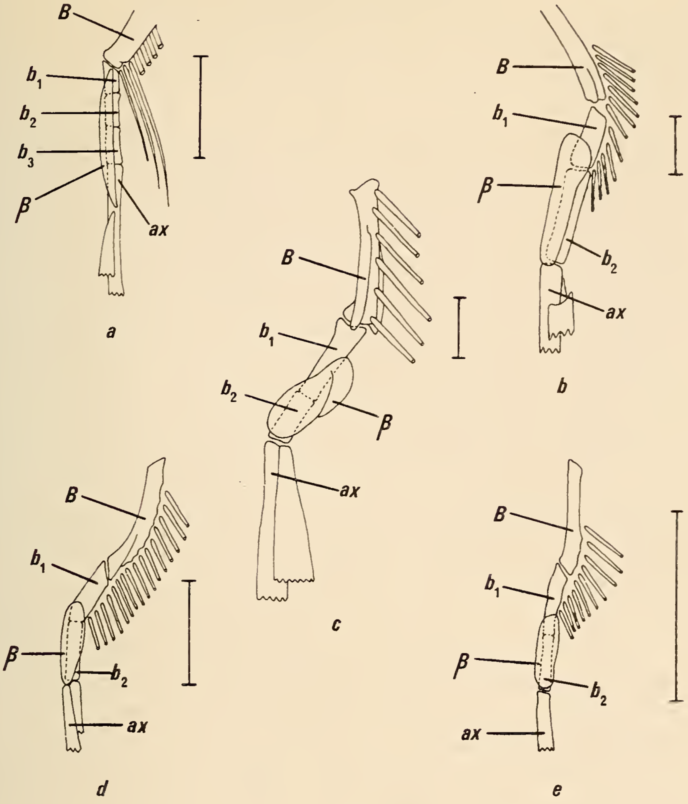

Fig. 15. Intermediate proximal segments of the claspers. a. *Rhinobatos annulatus*; b. *Bathyraja smithii*; c. *Raja clavata*; d. *Cruriraja parcomaculata*; e. *Anacanthobatis americanus*. Scale 2,0 cm.
B — basipterygium; b_1, b_2, b_3 — intermediate segments; β — beta cartilage; ax — axial cartilage.

Axial and terminal groups

The axial, dorsal marginal and ventral marginal cartilages are included in the axial group, but as it is the distal regions of these cartilages which are important, and since they extend into the terminal complex, they are described under this heading. The terminal group consists of three different types of cartilages: dorsal terminal cartilages, a series situated dorsally to the axial, to which some are joined; the ventral terminal cartilage, a single element which is ventrally situated and overlies the accessory terminals; the accessory terminal cartilages (Hulley 1966: fig. 3 G). The number of cartilages in the terminal group varies between seven and ten.

Huber (1901) and White (1937) suggest that the terminal (accessory) structures are constant within large groups of elasmobranchs, and Ishiyama

(1958) has discussed the specificity and evolutionary significance of the terminal group in Japanese rajids.

(1) *axial cartilage*

The axial cartilage, which is usually much less calcified than the other cartilages, forms the basic foundation of the clasper. At its junction with the b_2- and Beta-cartilages, it is almost cylindrical in cross-section, and it extends as a bar-like cartilage to terminate at the distal end of the clasper. From its proximal end to the level of the commencement of the glans, the axial is nearly completely enclosed by dorsal and ventral marginal cartilages, so as to form a tube on the outer lateral surface of the axial. This tube is the clasper groove.

The distal end of the axial cartilage is bluntly pointed in *Rhinobatos annulatus*, *Anacanthobatis americanus*, *Bathyraja smithii*, *Raja straeleni* and *R. clavata* (Figs 29, 32, 44, 45; Hulley 1966: fig. 3), but is expanded and spatulate in *Raja lanceorostrata*, *R. pullopunctata*, *R. doutrei*, *R. radiata*, *R. wallacei*, *R. confundens*, *R. caudaspinosa*, *R. leopardus*, *R. miraletus*, and *Myliobatis cervus* (Figs 30–31, 34–39, 46; Hulley 1966: fig. 5; 1969: fig. 3). In *Cruriraja parcomaculata*, *C. rugosa*, *C. triangularis* and *Anacanthobatis marmoratus* (Figs 40–43) the distal end is expanded laterally and recurved to form a J-shaped cartilage. The well-developed lateral expansion of the axial in *Raja alba* (Fig. 33) is not formed in a similar manner, and should rather be seen as further development of the spatulate type, through some intermediary like *Raja miraletus*.

(2) *dorsal marginal cartilage*

The dorsal marginal cartilage attaches tightly to the axial, starting where the axial is connected to the b_2/Beta joint, and runs along the outer lateral margin of the axial. Proximally, the cartilage is somewhat broadly pointed, but the distal region is characteristically expanded. Three different types may be recognized: the dorsal marginal may be truncate at its junction with the dorsal terminal 2 cartilage as in *Raja caudaspinosa*, *R. dissimilis*, *R. confundens*, *R. leopardus*; it may be asymmetrically bifurcate, with the larger of the two limbs developed from the inner lateral edge as in *Raja doutrei*, *R. pullopunctata*, *R. lanceorostrata*, *R. radiata*, *R. wallacei*, *Anacanthobatis americanus* and *Myliobatis cervus*; or may possess a marked distal elongation as in *Raja alba*, *R. clavata*, *R. straeleni*, *R. miraletus* and *Bathyraja smithii* (Figs 29, 32, 33; Hulley 1966: fig. 3; 1969: fig. 3). The distal elongation of the dorsal marginal into the clasper forms the dorsally situated pseudorhipidion. The extension is best developed in *Raja alba* (Fig. 33), where it narrows proximally, but becomes expanded distally and terminates in a blunt point at about half the length of the clasper glans. The distal elongation is shorter in *Raja miraletus* and is stepped to accommodate the dorsal terminal 2 cartilage (Hulley 1969: fig. 3). In *Raja clavata* and *R. straeleni*, it is only slightly stepped (Fig. 32; Hulley 1966: fig. 3).

A modified form of asymmetrically bifurcate type is found in the genus *Cruriraja* (Figs 40–42) and in *Anacanthobatis marmoratus*. In these species, it is the outer lateral edge which is elongate. This elongation is bluntly rounded in *Cruriraja parcomaculata* and *C. triangularis*, but is truncate in *C. rugosa*.

In *Rhinobatos annulatus* (Fig. 45) the dorsal marginal cartilage terminates in a bluntly rounded point.

(3) *ventral marginal cartilage*

The ventral marginal cartilage, unlike the dorsal marginal, arises some little distance posteriorly to the axial and b_2/Beta junction. It is a flat, tongue-like structure, whose outer lateral edge forms the ventral margin of the clasper groove. It extends further along the length of the clasper than the dorsal marginal cartilage, and distally is usually expanded and ventrally convex.

In the majority of the species examined, the terminal end of the ventral marginal cartilage is evenly curved. However, in *Bathyraja smithii* (Fig. 29) the outer lateral edge of the ventral marginal is elongate, extending almost to the distal end of the clasper. This distal prolongation of the cartilage forms the projection in the clasper glans.

The genus *Anacanthobatis* is unusual in that the distal end of the ventral marginal is truncate in *A. americanus* (Fig. 44), as it is in *Myliobatis cervus* (Fig. 46), and is anteriorly arched in *A. marmoratus*.

(4) *dorsal terminal* 1 *cartilage*

The dorsal terminal 1 cartilage ('cover-piece' of Jungersen 1899) is situated on the dorsal side of the clasper glans, usually partially overlying the other dorsal terminal cartilages. Ishiyama (1958), besides pointing out the species specificity of this cartilage, has shown that phylogenetic relationships may be based on its degree of development and orientation, together with its associated structure, the pseudosiphon. The pseudosiphon develops as a blindly ending sac, underlying the dorsal terminal 1. Dorsally the dorsal terminal 1 is flat and shield-like, but in some species it may be strongly curved medially to wrap around the inner margin of the axial cartilage. The *m. dilatator* is attached to the proximal edge of the dorsal terminal 1, but in *Raja miraletus*, *R. straeleni* and *R. clavata*, there is a proximal shelf (Figs 16 g–h), which serves as the area of attachment of the muscle. A smaller shelf is found in *Bathyraja smithii* (Fig. 16 a).

In the Rhinobatidae, e.g. *Rhinobatos annulatus* (Fig. 17 a) and *Rhinobatos schlegeli* (Ishiyama 1958: fig. 20), the dorsal terminal 1 is wholly situated on the ventral surface of the clasper, and is associated with the development of both the dorsal pseudosiphon and the ventral pseudosiphon. Similarly, in *Myliobatis cervus*, the dorsal terminal 1 is ventro-laterally positioned.

While the dorsal terminal 1 is dorsally situated in *Anacanthobatis marmoratus* (Fig. 17 g), it is positioned laterally in *A. americanus* (Fig. 17 h), so that the major portion of the cartilage is situated on the ventral surface of the clasper.

Amongst the Rajidae, seven types of dorsal terminal 1 cartilage may be distinguished. In *Bathyraja smithii* (Fig. 16 a), the dorsal terminal 1 is dorsally

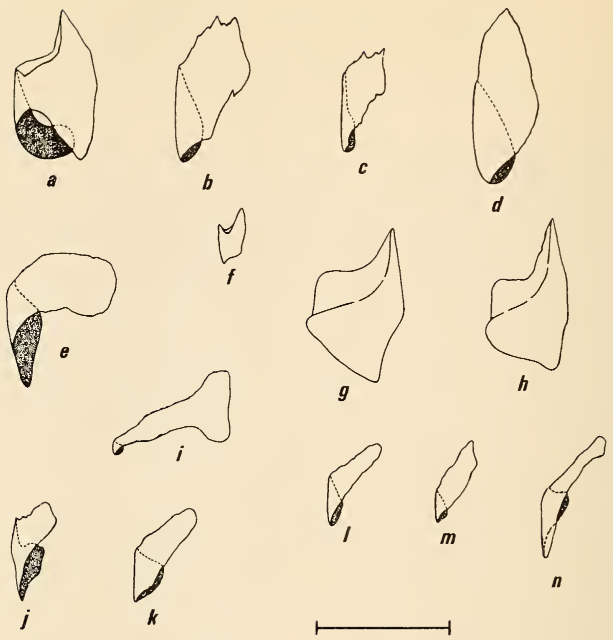

Fig. 16. Dorsal view of dorsal terminal 1 cartilages. Scale 4,0 cm.
a. *Bathyraja smithii*; b. *Raja doutrei*; c. *R. lanceorostrata*; d. *R. pullopunctata*; e. *R. alba*; f. *R. miraletus*; g. *R. clavata*; h. *R. straeleni*; i. *R. radiata*; j. *R. confundens*; k. *R. leopardus*; l. *R. dissimilis*; m. *R. caudaspinosa*; n. *R. wallacei*.

situated and shield-like, but it is markedly curved laterally and wraps around on to the ventral side, cf. *Bathyraja diplotaenia*, *B. parmifera* (= *B. simoterus*), *B. smirnovi* (Ishiyama 1958: fig. 8); in *Raja doutrei*, *R. lanceorostrata* and *R. pullopunctata* (Figs 16 b–d), the dorsal terminal 1 is shield-like dorsally, but is not so markedly curved along the inner lateral margin, and does not have the proximal shelf for the insertion of the *m. dilatator*; the dorsal terminal 1 in *Raja alba* (Fig. 16 a) is unique amongst the species examined in that curvature is well developed, while the dorsal area runs as a transverse band to the outer edge of the clasper; the cartilage in the species *Raja confundens*, *R. leopardus*, *R. dissimilis*, *R. caudaspinosa* and *R. wallacei* (Figs 16 j–n) have been classed together and appear to be not too different from that of *Raja alba*, but in these species the dorsal region of the cartilage is directed proximally; in *Raja radiata* (Fig. 16 i), there is virtually no ventral curvature, but the dorsal region of the cartilage is large and directed proximally, with an enlarged, hammer-shaped, outer lateral margin. The dorsal terminal 1 in *Raja miraletus*, *R. clavata* and *R. straeleni* (Figs 16 f–h) is carried almost entirely on the dorsal surface as a well-developed, shield-like structure with a proximal shelf. The similarity between the cartilages of *Raja clavata* and *R. straeleni* is marked.

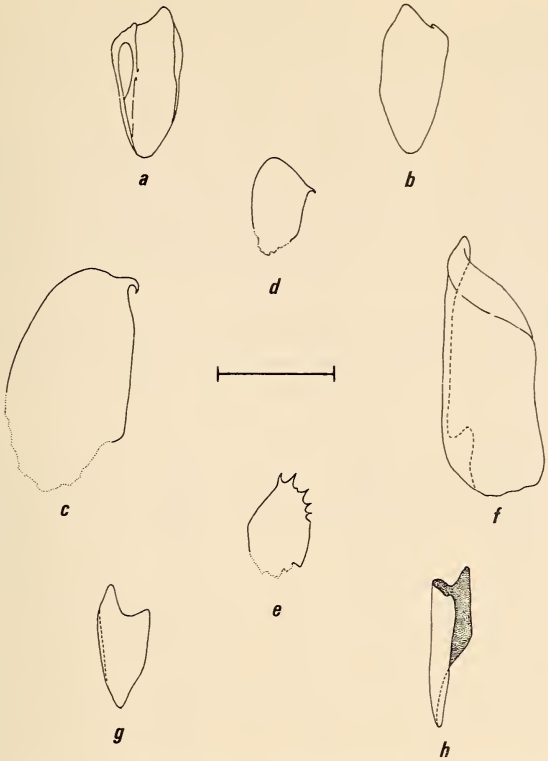

Fig. 17. Dorsal view of dorsal terminal 1 cartilage. Scale 1,0 cm.
a. *Rhinobatos annulatus*; b. *R. annulatus* (ventral view); c. *Cruriraja parcomaculata*; d. *C. triangularis*; e. *C. rugosa*; f. *Myliobatis cervus*; g. *Anacanthobatis marmoratus*; h. *A. americanus*.

A different type of cartilage is possessed by the genus *Cruriraja* (Figs 17 c–e). In this, the dorsal terminal 1 is situated within the short arm of the J-shaped axial, and only partially overlaps the dorsal terminal 2 proximally, so that the cartilage forms the dorsal wall of the clasper glans. Sharp points are developed on the proximo-lateral edge of the dorsal terminal 1, which are directly related to, and responsible for, the development of the thorn. A simple point is found in *Cruriraja parcomaculata* and *C. triangularis*, while a series of points is found in the North American species *C. rugosa*.

(5) *dorsal terminal 2 cartilage*

The dorsal terminal 2 is situated along the proximal dorsal border of the glans and is joined to the distal region of the dorsal marginal cartilage, or fits into a step in that cartilage, when the dorsal marginal has a well-developed distal extension (Hulley 1969: figs 3 A, C). The dorsal terminal 2, together with the dorsal terminals 3 and 4 (when present), extend distally as bar-like elements and form the framework of the dorsal lobe. Short, sharp processes may be developed on the outer lateral margin of the dorsal terminal 2, and these may protrude through the thin integument as the pecten.

The dorsal terminal 2 cartilage in *Rhinobatos annulatus* (Fig. 19 a) is not connected to the distal end of the dorsal marginal, but is tightly bonded along the inner lateral margin of that cartilage (Fig. 45). It is only slightly convex dorsally. A dorsally convex dorsal terminal 2 is also found in *Myliobatis cervus* (Fig. 19 d), but in this species it develops from the distal end of the dorsal marginal (Fig. 46).

As with the dorsal terminal 1, the dorsal terminal 2 cartilage can be divided into six types, although the grouping does not correspond with that of the dorsal terminal 1.

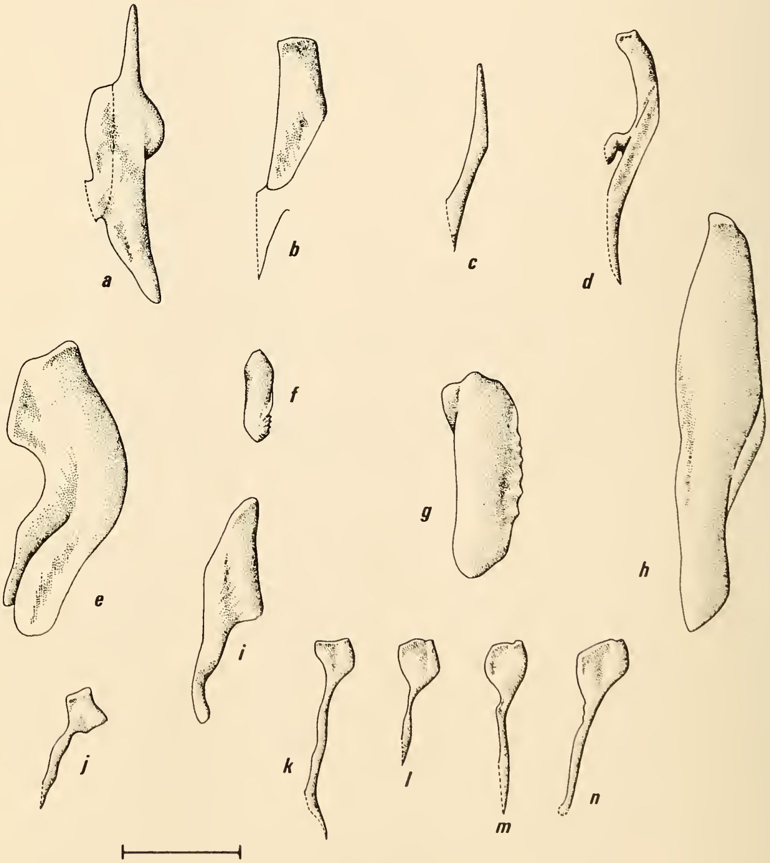

Fig. 18. Dorsal view of dorsal terminal 2 cartilage. Scale 2,0 cm.
a. *Bathyraja smithii* (dorsal terminal 2 and 3); b. *Raja doutrei*; c. *R. lanceorostrata*; d. *R. pullopunctata*; e. *R. clavata*; f. *R. miraletus*; g. *R. straeleni*; h. *R. alba*; i. *R. wallacei*; j. *R. radiata*; k. *R. dissimilis*; l. *R. caudaspinosa*; m. *R. confundens*; n. *R. leopardus*.

In *Bathyraja smithii* (Fig. 18 a) the dorsal terminal 2 arises at the distal end of the dorsal marginal and runs distally for a short distance, before turning laterally inward to become fused to the axial cartilage. Closely approximating to this type is the dorsal terminal 2 in *Raja pullopunctata*, *R. doutrei* and *R. lanceorostrata* (Figs 18 b–d), which becomes narrower proximally, to form a bar-like element. In *Raja doutrei* and *R. pullopunctata*, a short, cartilaginous bridge (terminal bridge) is developed, which attaches the dorsal terminal 2 to the axial. In *Raja lanceorostrata* (Fig. 31) the dorsal terminal 2 itself makes contact with the axial. A dorsal terminal 2/axial junction is also shown by the species *Raja radiata*, *R. dissimilis*, *R. caudaspinosa*, *R. confundens* and *R. leopardus* (Figs 18 j–n, 34, 36–39), but in these species the proximal end of the dorsal terminal is expanded, while the distal end is contracted. Although the dorsal terminal 2 is not attached to the axial in *Raja wallacei* (Figs 18 i, 35), it is similarly shaped. In this species the free end of the cartilage is responsible for the formation of the promontory. In *Raja miraletus* and *R. straeleni* the dorsal terminal 2 is flat and shield-like, with a series of protuberances situated on its outer lateral edge. An elongate cartilage is found in *Raja alba* (Fig. 18 h),

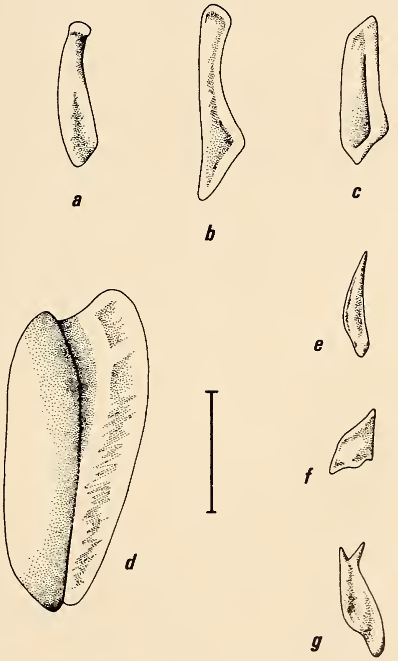

Fig. 19. Dorsal view of dorsal terminal 2 cartilage. Scale 1,0 cm.
a. *Cruriraja triangularis*; b. *C. parcomaculata*; c. *C. rugosa*; d. *Myliobatis cervus*; e. *Rhinobatos annulatus*; f. *Anacanthobatis marmoratus*; g. *A. americanus*.

which is similar to the cartilage in *R. miraletus* and *R. straeleni* (Figs 18 f, g), but does not form lateral processes. The dorsal terminal 2 is strongly curved in *Raja clavata* (Fig. 18 e) and is thickened along its side of greatest curvature, to form a flat ledge, which articulates with the dorsal terminal 1 cartilage. Although the dorsal terminal 2 appears to be species specific in *Cruriraja* species, they are of the same general type and are quite different from the structure of the cartilage in *Raja* species.

In the genus *Cruriraja*, the dorsal terminal 2 is a short and slightly curved bar-like element, which arises at the distal end of the dorsal marginal and terminates in a truncate tip, within the curvature offered by the dorsal terminal 1 (Figs 40–42).

As with the dorsal terminal 1, the dorsal terminal 2 cartilage in *Anacanthobatis marmoratus* (Fig. 19 f) and *A. americanus* (Fig. 19 g) is very dissimilar. In *A. marmoratus*, the dorsal terminal 2 is truncate and plate-like, while in *A. americanus* the proximal end of the tongue-like cartilage is bifurcate and the distal end is free and protrudes laterally from the axial.

(6) *dorsal terminal 3 cartilage*

This cartilage was found to be absent in *Cruriraja parcomaculata*, *C. triangularis*, *C. rugosa*, *Raja pullopunctata*, *R. miraletus*, *R. clavata*, *R. straeleni* and *Anacanthobatis americanus.*

In Rajidae, the dorsal terminal 3 extends distally from the dorsal terminal 2 cartilage and may either have a free, distal end, as in *Raja caudaspinosa*, *R. confundens*, *R. dissimilis*, *R. leopardus*, *R. wallacei* and *R. radiata* (Figs 20 c–h, 34–39),

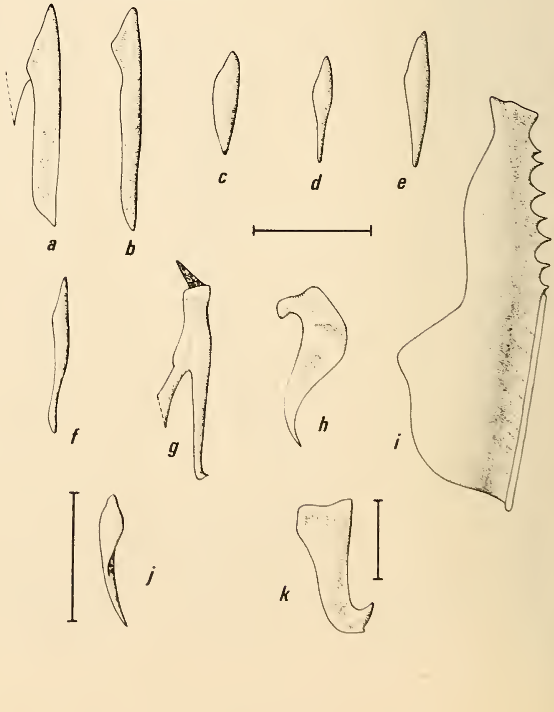

Fig. 20. Dorsal view of dorsal terminal 3 cartilage. Scale 2,0 cm. a. *Raja doutrei*; b. *R. lanceorostrata*; c. *R. caudaspinosa*; d. *R. dissimilis*; e. *R. confundens*; f. *R. leopardus*; g. *R. wallacei*; h. *R. radiata*; i. *R. alba*; j. *Rhinobatos annulatus* (scale 0,5 cm); k. *Anacanthobatis marmoratus* (scale 0,5 cm).

or the distal end may be fused to the expanded terminal end of the axial cartilage, as in *Raja doutrei* and *R. lanceorostrata* (Figs 20 a–b, 31, 32).

The dorsal terminal 3 cartilage in *Bathyraja smithii* (Fig. 18 a) is not firmly attached to the bluntly pointed axial. However, it is tightly bonded to the dorsal terminal 2 along its inner lateral margin, while its somewhat thickened, outer lateral edge forms the ridge in the clasper glans. The dorsal terminal 3 in *Raja lanceorostrata* and *R. doutrei* (Figs 20 a, b) is flat and spatulate, and arises either from the terminal bridge (*R. doutrei*) or directly from the dorsal terminal 2 (*R. lanceorostrata*).

The 'free-ended' dorsal terminal 3 species consist of two groups: (i) the distal region of the cartilage is curved laterally outward in a sharp point, forming the spur in *Raja radiata* and *R. wallacei* (Figs 34, 35); (ii) the cartilage is straight, and the free end is bluntly pointed, as in *R. caudaspinosa*, *R. confundens*, *R. dissimilis*, and *R. leopardus* (Figs 36–39). In the latter group the cartilage forms the outer lateral border of the distal cleft.

In *Rhinobatos annulatus* (Fig. 20 j) the dorsal terminal 3 is simple, while in *Myliobatis cervus* (Fig. 19 d) the cartilage is flat and attached along its inner lateral margin to the dorsal terminal 2 (Fig. 46), as in *Bathyraja smithii.* A spur is formed by the dorsal terminal 3 in *Anacanthobatis marmoratus* (Fig. 20 k).

(7) *dorsal terminal 4 cartilage*

This cartilage is present only in *Raja alba*, *R. radiata*, *R. dissimilis*, *R. caudaspinosa*, *R. confundens*, *R. leopardus* and *R. wallacei* cf. *R. fyllae*, *R. fullonica* (Stehmann 1970)—see discussion. In all these species, the dorsal terminal 4 attaches the dorsal terminal 3 to the axial, so completing the dorsal framework. On the basis of the attachment of the dorsal terminal 4 to the dorsal terminal 3, the cartilages may be divided into two groups. In the first, the dorsal terminal 4 attaches to the dorsal terminal 3 externally, some little distance behind the

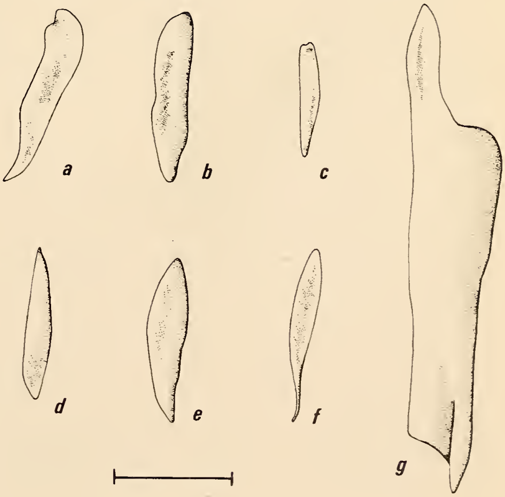

Fig. 21. Dorsal view of dorsal terminal 4 cartilage. Scale 2,0 cm. a. *Raja radiata*; b. *R. wallacei*; c. *R. caudaspinosa*; d. *R. confundens*; e. *R. leopardus*; f. *R. dissimilis*; g. *R. alba*.

dorsal terminal 3/dorsal terminal 2 junction, so that the distal end of the dorsal terminal 3 is free, e.g. *Raja radiata*, *R. caudaspinosa*, *R. confundens*, *R. dissimilis*, *R. leopardus* and *R. wallacei* (Figs 34–39). In the second group, e.g. *Raja alba* (Fig. 33), the dorsal terminal 4 is attached to the distal end of the dorsal terminal 3, thereby forming a link between this cartilage and the axial.

(8) *ventral terminal cartilage*

This cartilage was found to be absent only in *Anacanthobatis americanus*. The ventral terminal cartilage is located on the ventral side of the clasper, and extends from about the level of the distal end of the ventral marginal to the distal tip of the clasper. It therefore forms the ventral lobe of the clasper glans.

Amongst the Rajidae, *Bathyraja smithii* (Fig. 22 a) has the simplest ventral terminal cartilage. This is more or less spoon-shaped, with a somewhat pointed proximal extension and thickened distal region, so that it resembles the type usually associated with this genus (Ishiyama 1958: figs 10 B, E, F, H, I, L). The ventral terminal cartilages of *Raja doutrei*, *R. pullopunctata* and *R. lanceorostrata* have common characteristics and may be grouped together. In these species (Figs 22 b–d) the cartilage may be divided into three areas: the outer lateral margin is well developed and is dorsally convex, forming the shield of the glans; there is an anterior notch, which attaches to the accessory terminal 1 cartilage; the distal region is expanded on its inner lateral margin and this plate-like area folds around the axial, so that the ventral terminal attains a J-shape. The outer lateral margin is narrower and flat in *Raja miraletus*, *R. straeleni* and *R. clavata* (Figs 22 e–g), so that in these species the shield is not well developed. Although the medio-distal inner margin of the cartilage is expanded to wrap around the axial (Hulley 1966: fig. 3 G; Figs 22 e–g), the distal end of the cartilage is well developed and forms a structure which resembles the foot of a bivalve mollusc. This distal end forms the funnel of the glans. There is no anterior notch.

The ventral terminal in *Raja alba* (Fig. 22 h) appears to be unique in that, while the inner median lateral edge of the cartilage is expanded to curve around the axial cartilage, the outer lateral margin is well developed and dorsally convex.

Unlike the above, the ventral terminals in the following rajids are different in that neither the distal tip, nor the inner lateral margin are expanded to encompass the axial. The anterior notch, for attachment to the accessory terminal 1, is shifted posteriorly and is situated at about half the length of the cartilage. Furthermore, it is the proximal region of the ventral terminal which is expanded, and in the species *Raja caudaspinosa*, *R. confundens*, *R. dissimilis*, *R. leopardus* and *R. wallacei* (Figs 22 j–n) is characterized by an inner lateral expansion, cf. projection of *Raja lintea* (Leigh-Sharpe 1924: fig. 6). On the basis of the above, *Raja caudaspinosa*, *R. confundens*, *R. dissimilis*, *R. leopardus* and *R. wallacei* have been grouped together, and while *R. radiata* is somewhat similar, it has been kept separate because of its unique shape and its median notch (Fig. 22 i).

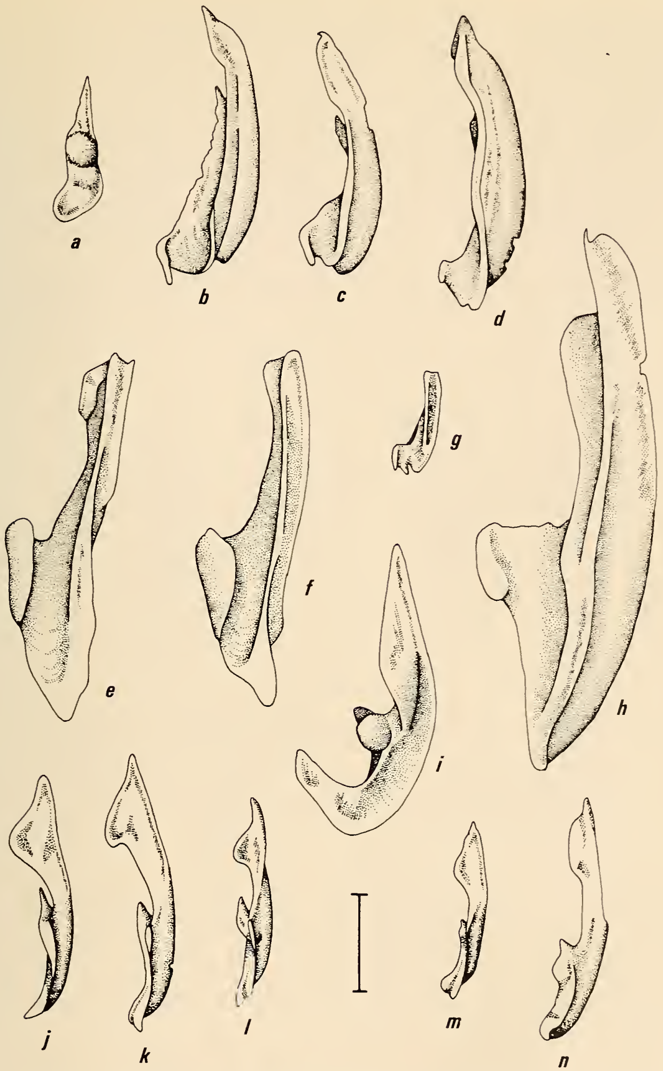

Fig. 22. Dorsal view of ventral terminal cartilage. Scale 2,0 cm. a. *Bathyraja smithii*; b. *Raja doutrei*; c. *R. lanceorostrata*; d. *R. pullopunctata*; e. *R. clavata*; f. *R. straeleni*; g. *R. miraletus*; h. *R. alba*; i. *R. radiata*; j. *R. confundens*; k. *R. leopardus*; l. *R. dissimilis*; m. *R. caudaspinosa*; n. *R. wallacei*.

Once again the ventral terminal in the genus *Cruriraja* is more or less constant in shape, although it appears to be species specific. In these species (Figs 23 a–c), a point is developed on the proximal outer lateral edge of the narrow shield. This is the eperon. The notch is situated anteriorly in all, but in *C. triangularis* the distal region is bifurcate and in *C. rugosa* it is expanded.

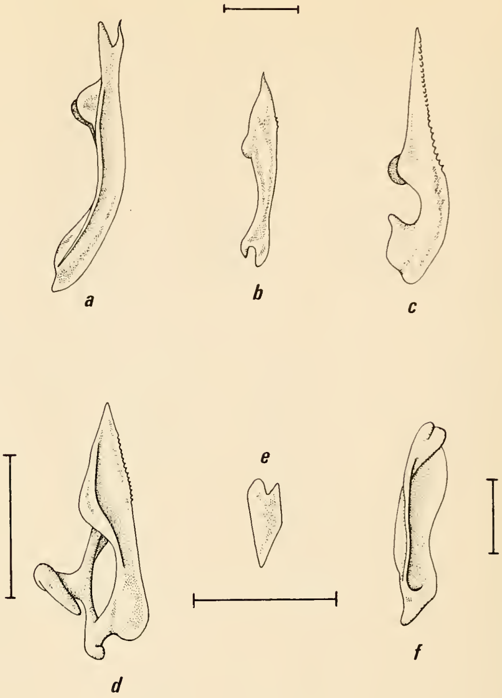

Fig. 23. Dorsal view of ventral terminal cartilage. Scale 1,0 cm.
a. *Cruriraja parcomaculata*; b. *C. triangularis*; c. *C. rugosa*; d. *Anacanthobatis marmoratus*; e. *Rhinobatos annulatus*; f. *Myliobatis cervus*.

The ventral terminal in *Anacanthobatis marmoratus* (Fig. 23 d) is unusual. It possesses a well-developed outer lateral edge, which forms the shield, and which is serrate, as in some *Cruriraja* species. Medially the cartilage is expanded and runs around the axial, as in *Raja alba*. However, in *Anacanthobatis marmoratus* the inner lateral plate is windowed.

(9) *accessory terminal* 1 *cartilage*

In all Batoidei the accessory terminal 1 arises at the distal end of the ventral marginal cartilage, but its form in the Rhinobatoidea and Myliobatoidea (Figs 45, 46) is quite different from that in the Rajoidea, although the accessory terminal 1 in *Anacanthobatis marmoratus* and *A. americanus* resembles that of *Rhinobatos annulatus* (Figs 25 c–e) and *Myliobatis cervus* (Fig. 46), particularly in its sharp, pointed distal end. The accessory terminal 1 is closely associated with the accessory terminal 2, although in *Rhinobatos annulatus*, *Myliobatis cervus* and *Bathyraja smithii* only one accessory terminal cartilage is present. The distal end of the accessory terminal 1 has been termed the sentinel in all cases in which this cartilage manifests itself within the glans, except in the abovementioned species, in which it is variously termed claw and knife, depending on its degree of development, cf. Stehmann (1970). The distal end of the accessory terminal 1 cartilage varies in shape from elongate, sharp-pointed to expanded and flattened. In *Cruriraja* species, there is a lateral process, which develops at about half the length of the cartilage, in the form of the knob. This consists of a flattened protuberance in *C. rugosa* (Fig. 25 f), a series of four blunt lobes in *C. parcomaculata* (Fig. 25 a, a^1), or a sharp, recurved spine in *C. triangularis* (Fig. 25 b, b^1).

The accessory terminal in *Bathyraja smithii* (Fig. 24 a) is unusual and quite

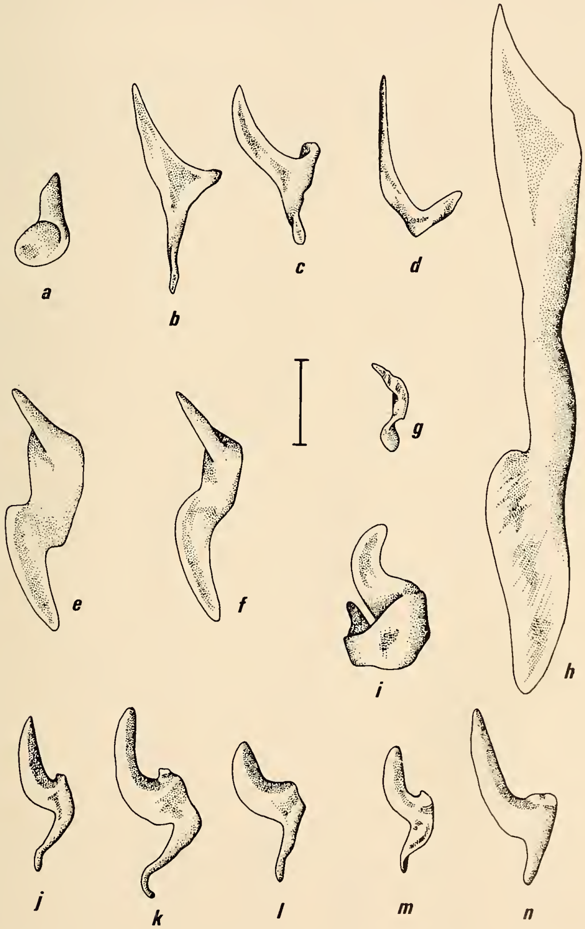

Fig. 24. Ventral view of accessory terminal 1 cartilage. Scale 2,0 cm.
a. *Bathyraja smithii*; b. *Raja doutrei*; c. *R. lanceorostrata*; d. *R. pullopunctata*; e. *R. clavata*; f. *R. straeleni*; g. *R. miraletus*; h. *R. alba*; i. *R. radiata*; j. *R. confundens*; k. *R. leopardus*; l. *R. dissimilis*; m. *R. caudaspinosa*; n. *R. wallacei*.

unlike the cartilage in other rajid species. The cartilage is fan-shaped with a blade-like posterior margin, similar in shape to the accessory terminal in *Rhinoraja odai* and *Rhinoraja longicauda* (Ishiyama 1958: fig. 11). In all other rajids, the accessory terminal 1 cartilage is Y-shaped, although in *Raja clavata*, *R. straeleni*, *R. miraletus* and *R. alba* (Figs 24 e–h) there appears to be a single arm. Ishiyama (1958) has commented on the change from a symmetrical to an asymmetrical shape.

Furthermore, Ishiyama (1958) has grouped the accessory terminal 1 according to the shape of the distal region of the cartilage. However, in this study the accessory terminal 1 has been grouped on the basis of general overall appearance. Excluding the species *Bathyraja smithii*, five types of cartilages can be identified in southern African rajids.

In *Raja pullopunctata*, *R. doutrei* and *R. lanceorostrata*, the cartilage is of asymmetrical Y-shape, with the posterior arm varying from elongate and pointed (*R. doutrei*, Fig. 24 b) to a small blunt process (*R. pullopunctata*, Fig. 24 d).

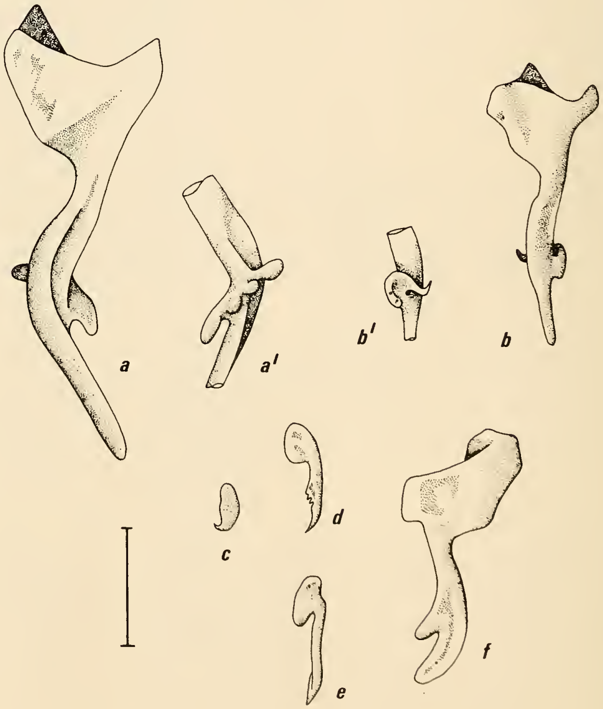

Fig. 25. Ventral view of accessory terminal 1 cartilage. Scale 1,0 cm.
a. *Cruriraja parcomaculata*; a^1. *C. parcomaculata* (dorsal view); b. *C. triangularis*; b^1. *C. triangularis* (dorsal view); c. *Rhinobatos annulatus*; d. *Anacanthobatis marmoratus*; e. *A. americanus*; f. *Cruriraja rugosa*.

The accessory terminal 1 in *Raja clavata*, *R. straeleni* and *R. miraletus* (Figs 24 e–g) is characterized by a single, outwardly directed proximal arm and a very well-developed and dorso-ventrally flattened distal blade. Although the form of the cartilage is somewhat similar in *Raja alba* (Fig. 24 h), it has not been included with *R. clavata* because of its elongate- rather than Z-shape, and because of the lack of a distinguishable proximal arm.

The U-shaped accessory terminal 1 in *Raja radiata* is unique (Fig. 24 i) and quite unlike the Y-form of the cartilage in *Raja confundens*, *R. leopardus*, *R. dissimilis*, *R. caudaspinosa* and *R. wallacei* (Figs 24 j–n), whose anterior limbs resemble that of *R. lanceorostrata*, and yet whose general form is quite different. The species specificity of the posterior extension should be noted.

(10) *accessory terminal 2 cartilage*

This cartilage, like the accessory terminal 1, arises at the distal end of the ventral marginal cartilage. It is situated on the median side of the accessory terminal 1. Although it may possess a median, lateral process, which can form the boss (*Cruriraja parcomaculata*, Fig. 27 a, a^1), it is the distal end which is

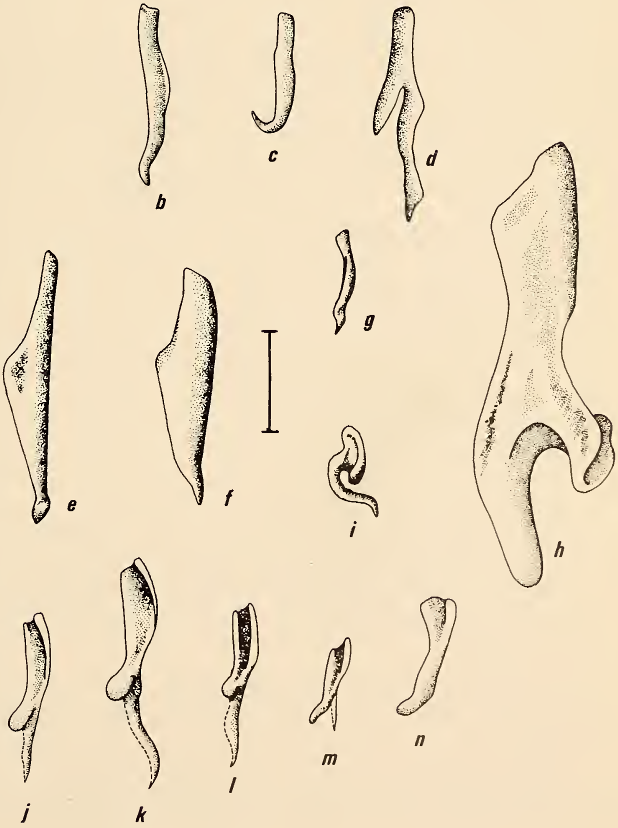

Fig. 26. Ventral view of accessory terminal 2 cartilage. Scale 2,0 cm.
b. *Raja doutrei*; c. *R. lanceorostrata*; d. *R. pullopunctata*; e. *R. clavata*; f. *R. straeleni*; g. *R. miraletus*; h. *R. alba*; i. *R. radiata*; j. *R. confundens*; k. *R. leopardus*; l. *R. dissimilis*; m. *R. caudaspinosa*; n. *R. wallacei*.

important and which forms the spike. An accessory terminal 2 cartilage is absent in *Rhinobatos annulatus*, *Myliobatis cervus* and *Bathyraja smithii*.

Groupings similar to those shown by the accessory terminal 1 cartilage can be seen. In the species *Raja doutrei*, *R. pullopunctata* and *R. lanceorostrata* (Figs 26 b–d) the accessory terminal 2 projects distally as a simple rod, which may be hooked distally, and may or may not possess an attachment process. The cartilage is strongly united with the accessory terminal 1 in *Raja clavata* (Hulley 1966: fig. 3 E) and *R. straeleni*, while in *R. miraletus* the association does not appear to be that marked (Hulley 1969). Although not strongly united with the accessory terminal 1, the accessory terminal 2 cartilage in *Raja radiata* is somewhat curled (Fig. 26 i), so as to lie within the cavity of the accessory terminal 1 (Fig. 34). The accessory terminal 2 in *Raja alba* (Fig. 26 h) is simple, with a shortened distal end, so that a spike is not formed in the glans. It has a process on its inner lateral margin, which butts against the axial cartilage. The species *Raja dissimilis*, *R. caudaspinosa*, *R. confundens*, *R. leopardus* and *R. wallacei* possess a characteristically shaped accessory terminal 2 (Figs 26 j–n).

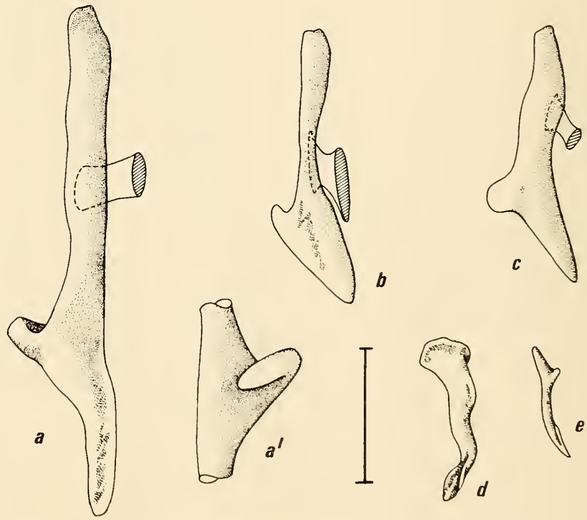

Fig. 27. Ventral view of accessory terminal 2 cartilage. Scale 1,0 cm.
a. *Cruriraja parcomaculata*; a^1. *C. parcomaculata* (dorsal view); b. *C. triangularis*; c. *C. rugosa*; d. *Anacanthobatis marmoratus*; e. *A. americanus*.

In the genus *Cruriraja* (Figs 27 a–c), the cartilage is elongate, and in the three species examined a lateral process was found. Distally the cartilage is rounded.

A similarly shaped accessory terminal 2 cartilage is found in *Anacanthobatis marmoratus* (Fig. 27 d), except that there is no lateral process and the flattened, distal region is curled to form a spoon-shaped end. In *Anacanthobatis americanus* (Fig. 27 e), the accessory terminal 2 is Y-shaped, and similar in appearance to the accessory terminal 1 cartilage in this species.

(11) *accessory terminal* 3 *and* 4 *cartilages*

These cartilages are present only in *Raja clavata*, *R. straeleni* and *R. miraletus*, and form the signal of the clasper glans. As with other accessory terminal cartilages, they are attached at the distal end of the ventral marginal, more ventral than the attachment of the accessory terminal 1 and 2 cartilages. In *Raja miraletus* (Fig. 28 c) there is a single cartilaginous element, the accessory terminal 3, while in *R. clavata* and *R. straeleni* (Figs 28 a–b) two cartilages are present. In the latter two species, the accessory terminal 4 is movable on the accessory terminal 3.

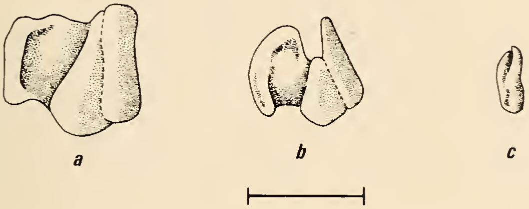

Fig. 28. Ventral view of accessory terminals 3 and 4.
Scale 2,0 cm.
a. *Raja clavata*; b. *R. straeleni*; c. *R. miraletus*.

VERTEBRAL COUNT

Vertebral numbers have been employed as taxonomic characters in teleosts (Bailey & Gosline 1955; Lagler *et al.* 1962). Their possible use in elasmobranch taxonomy was reviewed by Springer & Garrick (1964), while their species specificity in Japanese rajids has been investigated by Ishiyama (1952, 1958) and in European rajid species by Stehmann (1970). Vertebral counts for South African west and south coast Rajidae have been given by Hulley (1970). Krefft (1968*a*) has analysed the terminology, and has proposed a standard method for distinguishing the various groups of vertebrae.

In rajids, the vertebrae may be divided into two groups, trunk (Vtr) and predorsal caudal (Vprd) vertebrae, of which the latter appears to be more suitable for taxonomic purposes. The number of predorsal caudal vertebrae is not species specific (Ishiyama, 1958), although the count may, in some cases, be used to distinguish between closely related species (Hulley 1970; Stehmann 1970).

Interpreting the predorsal caudal count according to the method of Hubbs & Hubbs (1953), Ishiyama (1958) recognizes two forms of rajids, the 'northern' form (*Bathyraja* and *Rhinoraja*) with more than 61–62 Vprd, and the 'southern' form (*Raja*) with less than 61–62 Vprd. Stehmann (1970) can find no clear-cut distinction between the two genera, *Bathyraja* and *Raja*, in European species, but

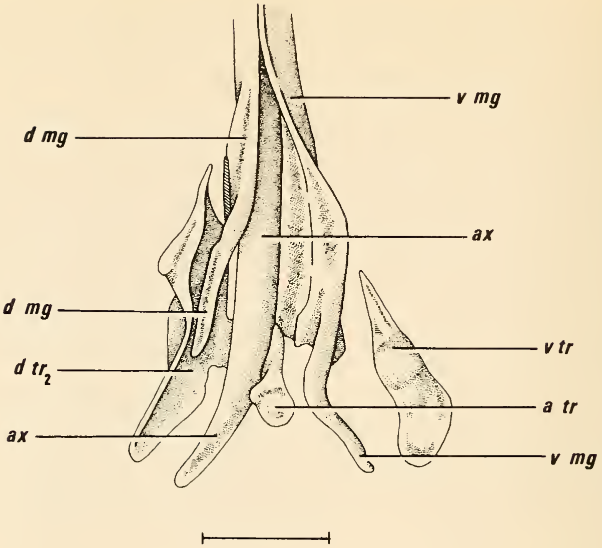

Fig. 29. *Bathyraja smithii.* Cartilages of right clasper (exploded) with $d.tr_1$ removed. Scale 2,0 cm.
a.tr.—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg.—ventral marginal; v.tr—ventral terminal.

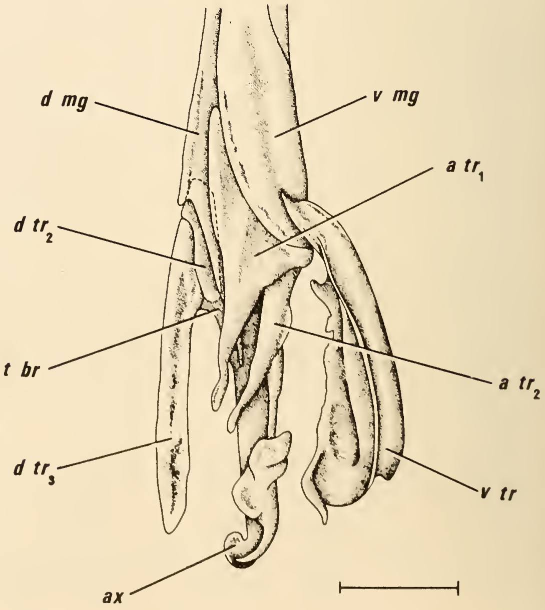

Fig. 30. *Raja doutrei.* Cartilages of right clasper (exploded) with $d.tr_1$ removed. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; dm.g—dorsal marginal; d.tr—dorsal terminal; t.br—terminal bridge; v.mg—ventral marginal; v.tr—ventral terminal.

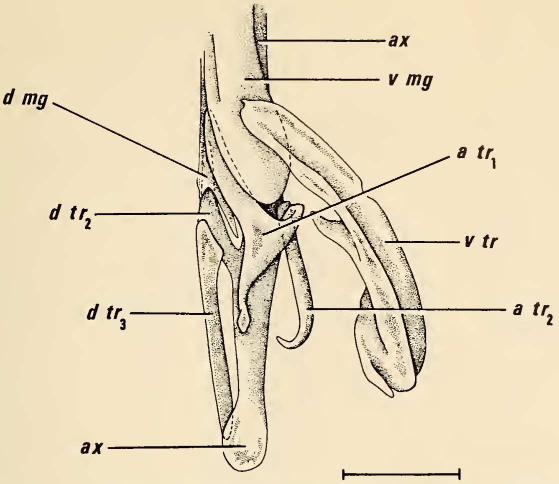

Fig. 31. *Raja lanceorostrata.* Cartilages of right clasper (exploded) with d.tr$_1$ removed. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal; v.tr—ventral terminal.

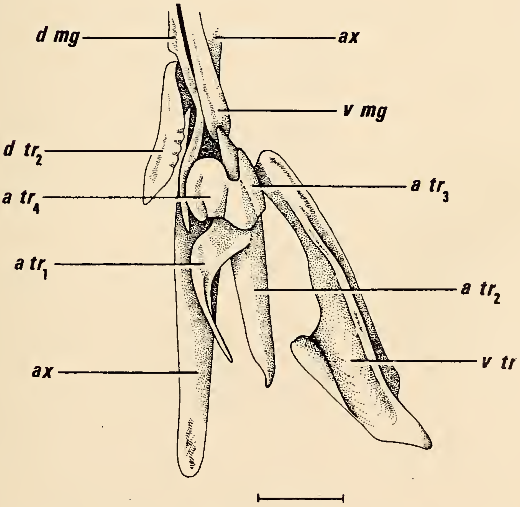

Fig. 32. *Raja straeleni.* Cartilages of right clasper (exploded) with d.tr$_1$ removed. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal; v.tr—ventral terminal.

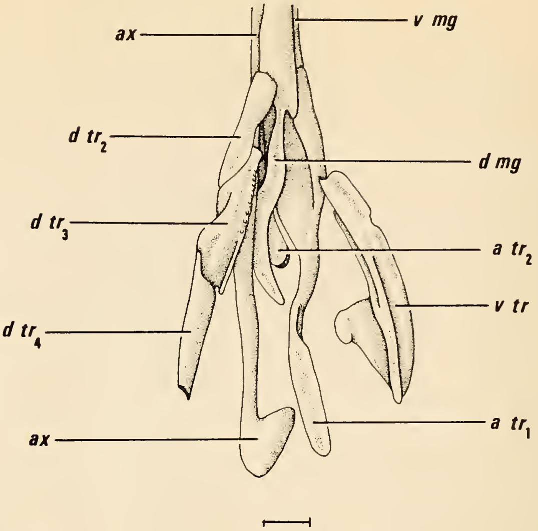

Fig. 33. *Raja alba.* Cartilages of right clasper (exploded) with d.tr_1 removed. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal; v.tr—ventral terminal.

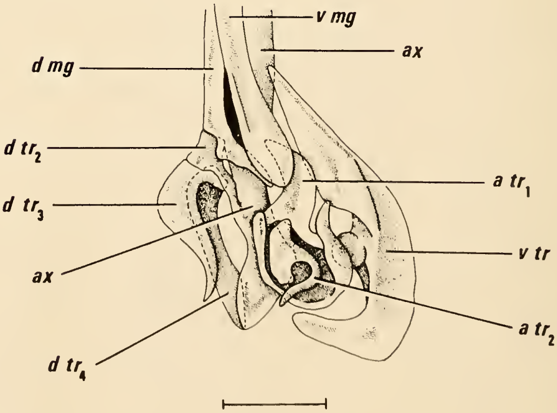

Fig. 34. *Raja radiata.* Cartilages of right clasper (exploded) with d.tr_1 removed. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal; v.tr—ventral terminal.

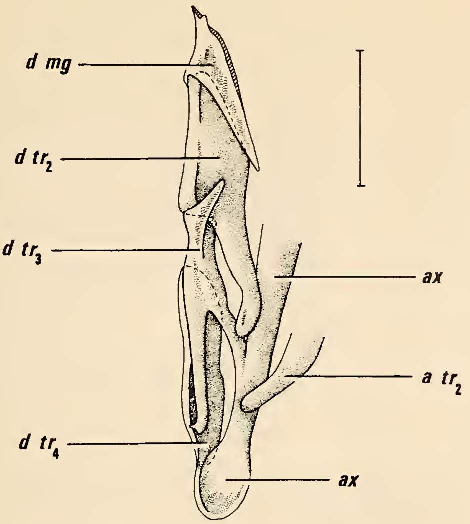

Fig. 35. *Raja wallacei*. Ventral view of cartilages of right clasper. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal.

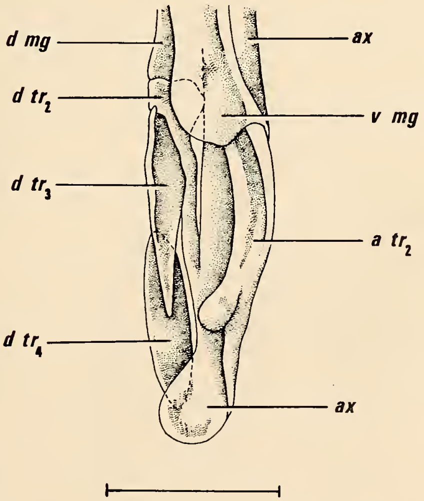

Fig. 36. *Raja confundens*. Ventral view of cartilages of right clasper, with d.tr$_1$, a.tr$_1$ and v.tr removed. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal.

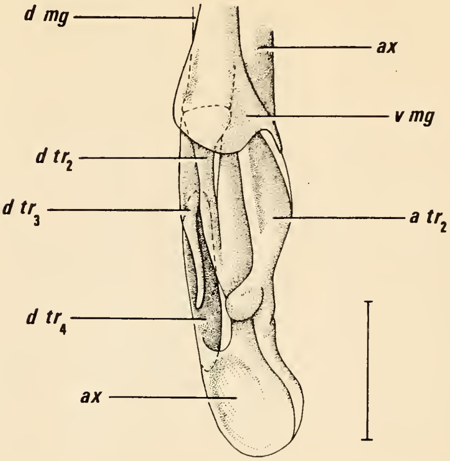

Fig. 37. *Raja leopardus.* Ventral view of cartilages of right clasper, with $d.tr_1$, $a.tr_1$ and v.tr removed. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal.

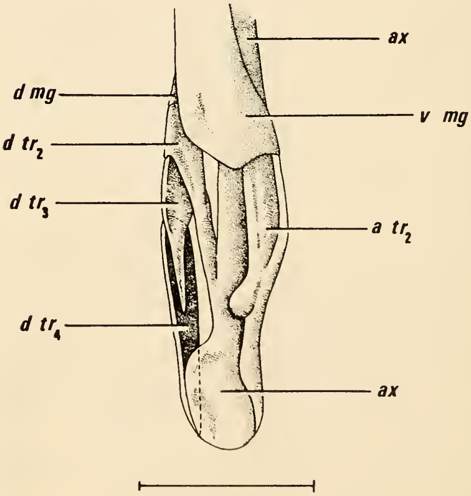

Fig. 38. *Raja dissimilis.* Ventral view of cartilages of right clasper, with $d.tr_1$, $a.tr_1$ and v.tr removed. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal.

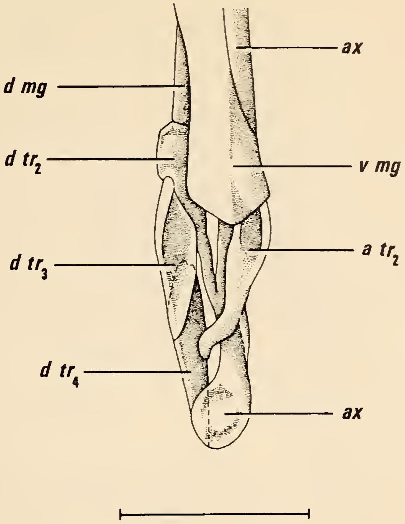

Fig. 39. *Raja caudaspinosa*. Ventral view of cartilages of right clasper, with d.tr_1, a.tr_1 and v.tr removed. Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal.

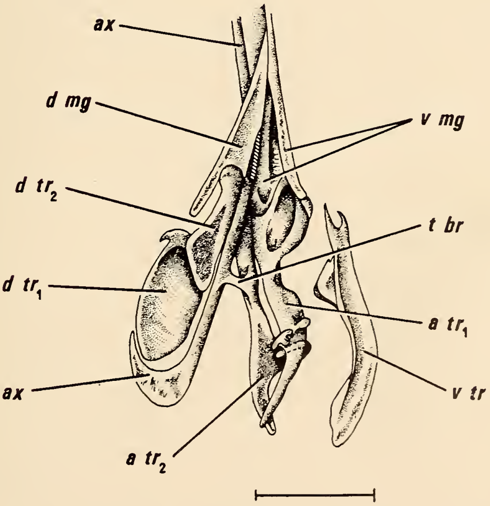

Fig. 40. *Cruriraja parcomaculata*. Cartilages of right clasper (exploded). Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; t.br—terminal bridge; v.mg—ventral marginal; v.tr—ventral terminal

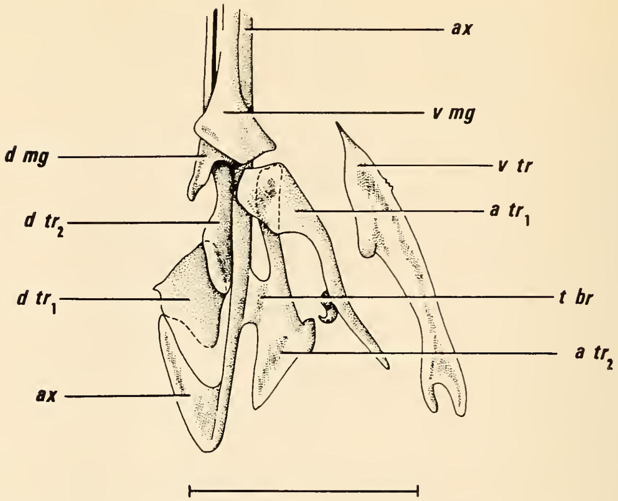

Fig. 41. *Cruriraja triangularis*. Cartilages of right clasper (exploded). Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; t.br—terminal bridge; v.mg—ventral marginal; v.tr—ventral terminal.

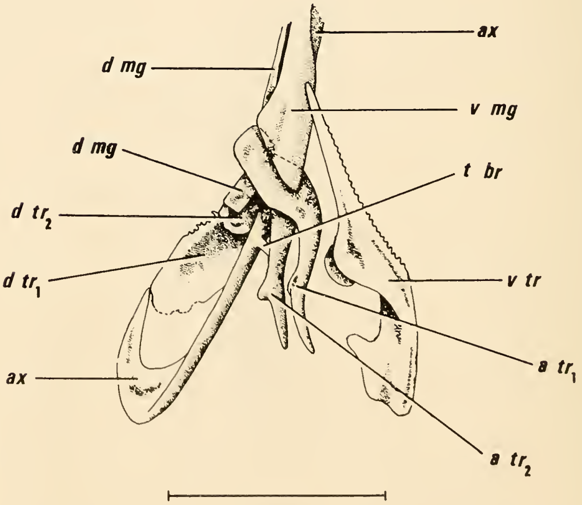

Fig. 42. *Cruriraja rugosa*. Cartilages of right clasper (exploded). Scale 2,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; t.br—terminal bridge; v.mg—ventral marginal; v.tr—ventral terminal.

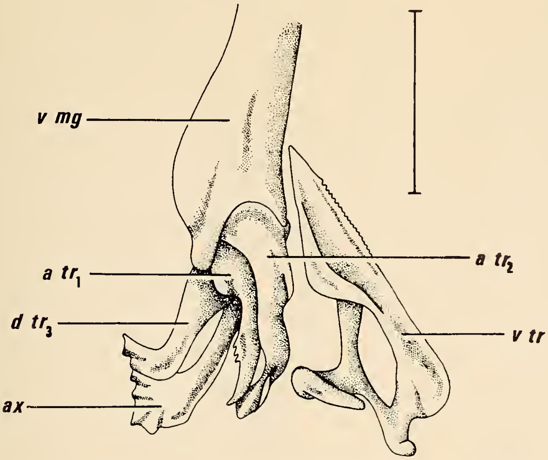

Fig. 43. *Anacanthobatis marmoratus*. Cartilages of right clasper (exploded) with d.tr$_1$ removed. Scale 1,0 cm. a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal; v.tr—ventral terminal.

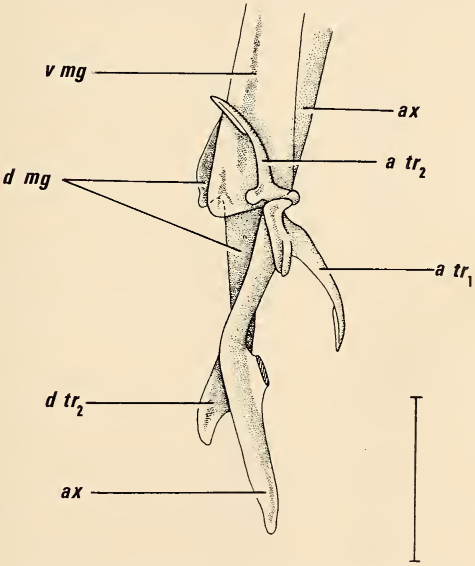

Fig. 44. *Anacanthobatis americanus*. Ventral view of cartilages of right clasper with d.tr$_1$ removed. Scale 1,0 cm.
a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal.

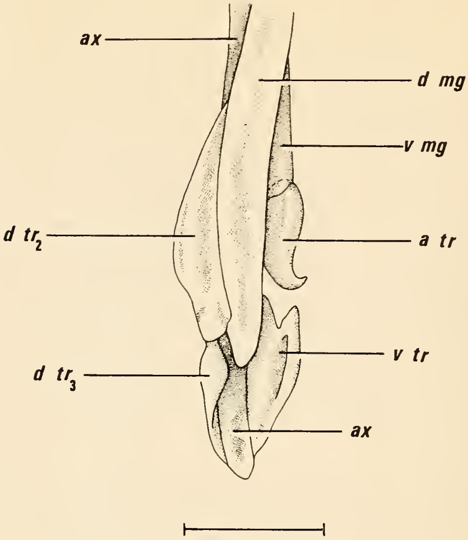

Fig. 45. *Rhinobatos annulatus.* Dorsal view of cartilages of right clasper, with d.tr$_1$ removed. Scale 0,5 cm.

a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal; v.tr—ventral terminal.

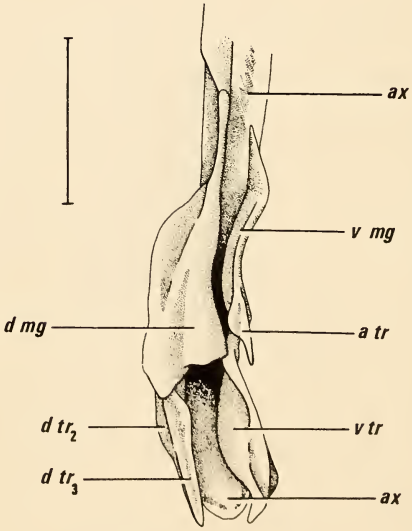

Fig. 46. *Myliobatis cervus.* Lateral view of cartilages of right clasper with d.tr$_1$ removed. Scale 2,0 cm.

a.tr—accessory terminal; ax—axial; d.mg—dorsal marginal; d.tr—dorsal terminal; v.mg—ventral marginal; v.tr—ventral terminal.

divides them into four groups. The group limits appear to be arbitrary and are exceeded by some of the species (Stehmann 1970: fig. 14), so that this clustering is artificial and bears no resemblance to the groupings suggested by clasper structure and cranial anatomy. The picture is further complicated by the fact that, as in teleosts (Tester 1938; Tåning 1950; Post 1968), there appears to be some correlation between water temperature and vertebral number in skates (Ishiyama 1958). However, Stehmann (1970) states that an intra-specific dependence of the number of predorsal caudal vertebrae on water temperature is not noticeable in eastern North Atlantic species. In the case presented, i.e. *Raja miraletus*, it may be that we are dealing here with isothermic distribution rather than temperature differences based on geographic distribution.

Predorsal caudal vertebral counts can be used in the interpretation of the phylogeny of rajids. Ishiyama (1958: 237) has pointed out that 'the variation in vertebral count in each group of species (as ascertained from clasper structure) can be considered corresponding with phylogenetic progression along each branch' and has shown that with evolution there is a trend in reduction in number of predorsal caudal vertebrae. It is within this context that the predorsal caudal count of southern African rajids will be discussed.

TABLE 1

Predorsal caudal vertebral counts (Vprd) for southern African Rajidae.

Species	No. of specimens	Range	Mean
B. smithii	6	68–71	69,2
R. straeleni	4	48–52	49,3
R. clavata	10	45–53	47,7
R. miraletus	17	44–52	48,5
R. alba	6	62–67	64,0
R. pullopunctata	14	50–58	53,4
R. doutrei	4	43–49	46,0
R. springeri	3	53–56	55,0
R. stenorhynchus	1	—	49,0
R. lanceorostrata	2	56–57	56,5
R. robertsi	1	—	55,0
R. radiata	2	58–62	60,0
R. wallacei	10	64–74	69,0
R. ravidula	3	69–70	69,3
R. dissimilis	3	65–69	67,0
R. caudaspinosa	15	66–73	67,0
R. leopardus	7	55–58	56,9
R. confundens	5	55–63	59,2
R. spinacidermis	3	60–65	62,7
C. parcomaculata	6	66–69	67,8
C. triangularis	4	65–70	67,3

The predorsal caudal vertebral count for southern African species is given in Table 1, and is represented graphically in Figure 47, in subgeneric groupings. Vprd counts for *Raja miraletus* and *R. straeleni* given by Krefft (1968*a*) are incorporated in the results.

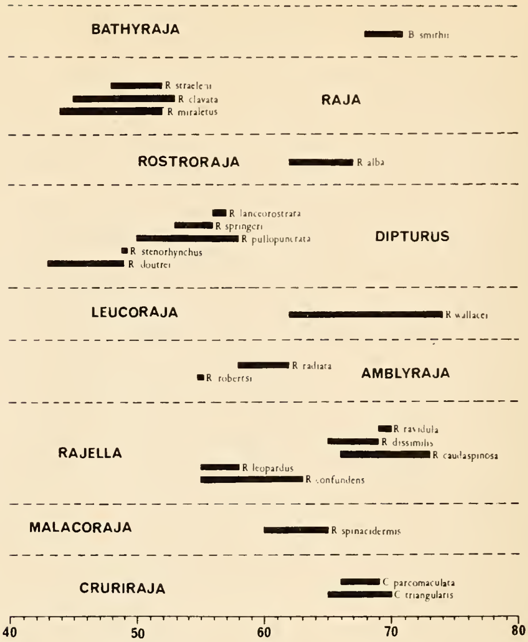

Fig. 47. Ranges in number of predorsal caudal vertebrae (Vprd) in southern African Rajidae.

Neurocranium and Rostral Cartilages

In order to establish the phylogenetic positions of suborders within the Batoidei, comparative anatomical studies on various neurocrania have been made (Gegenbaur 1872; Parker 1879; Garman 1913; Holmgren & Stensio 1936; Davies 1948; Melouk 1949; El-Tourbi & Hamdy 1959; Gohar & Bayoumi 1959; Hamdy 1964) and these have been supplemented by developmental studies (Parker 1879; De Beer 1926, 1932, 1937; Holmgren 1940, 1941; Hamdy 1956).

From a taxonomic viewpoint at the generic level, Bigelow & Schroeder (1948) studied the X-ray structure of *Psammobatis*, *Sympterygia* and some *Raja* species, with particular reference to the rostral projection and the degree of forward extension of the anterior radials of the pectoral fins. This resulted in the distinction of a new genus *Breviraja*. Following on this, Ishiyama (1952, 1958, 1968) recognized this genus in Japanese rajids and was able to show that a further new genus, *Rhinoraja*, could be established on rostral characters.

Subsequently, Ishiyama & Hubbs (1968) pointed out that the Pacific brevirajid species were distinct from the Atlantic species, not only in terms of clasper structure, but also in the shape and size of the rostral cartilage and rostral appendices. They therefore defined a new genus, *Bathyraja*, confining it solely to the Pacific region. However, this genus has now been recognized in the

North Atlantic (Stehmann 1970) and in the southern African region (Hulley 1970).

Further differences in the anatomy of the neurocrania of Japanese rajids were found by Ishiyama (1958), who showed a certain degree of species specificity in the shape and extension of the anterior and posterior fontanelles. However, Heintz (1962) found that the cartilaginous neurocranium could be modified by external factors, and noted differences only in the anterior fontanelle, orbital and otic regions of the neurocrania of *Raja batis*, *R. nidarosiensis* and *R. oxyrhynchus*, so that on the basis of structure alone it was impossible to draw any conclusions of the relationship of the three species.

On the other hand, Stehmann (1970) found that while species specificity may not necessarily be evident from cranial structure, there appeared to be certain parts, which could be used as auxiliary characters in the grouping of the species within the proposed subgenera. These included:

1. The shape and orientation of the nasal capsules with regard to the median axis of the skull.
2. The appearance and size of the *processus praeorbitalis*, including the *crista praeorbitalis*.
3. The form of the *regio orbito-temporalis*.
4. The size and position of the jugal arches.
5. The form and position of the anterior and posterior fontanelles.

Differences in cranial morphometry for taxonomic use were suggested by Ishiyama (1958) and some 18 measurements have now been proposed as standards (Hubbs & Ishiyama 1968). However, both Heintz (1962) and Stehmann (1970) find that these possess no species specificity, although Stehmann (1970) finds that the length of the rostrum in comparison with the length of the cranium can be used for grouping the species. The course of the hypothetical line, drawn from the tip of the rostrum and over the *Foramen ophthalmicus profundus V* to the otic region (Stehmann 1970) is obviously some complex function of the rostral length/cranial width, and is difficult to interpret as a single character.

Description

Descriptions are based mainly on neurocrania which have been prepared. However, in cases where this was not possible, some results, such as general shape, orientation of the nasal capsules, form of the anterior and posterior fontanelles and size of the jugal arches, have been obtained from X-ray photographs. Details of the cranial anatomy of *Rhinobatos halavi* have been given by El-Tourbi & Hamdy (1959) and are used in this description.

The neurocranium is a violin-shaped structure, which is dorso-ventrally compressed and is contricted at the orbital region. The nasal capsules are fused to this anteriorly and the auditory capsules posteriorly. The rostral bar projects from the mid-region as a hard bar, to which are attached the rostral appendices.

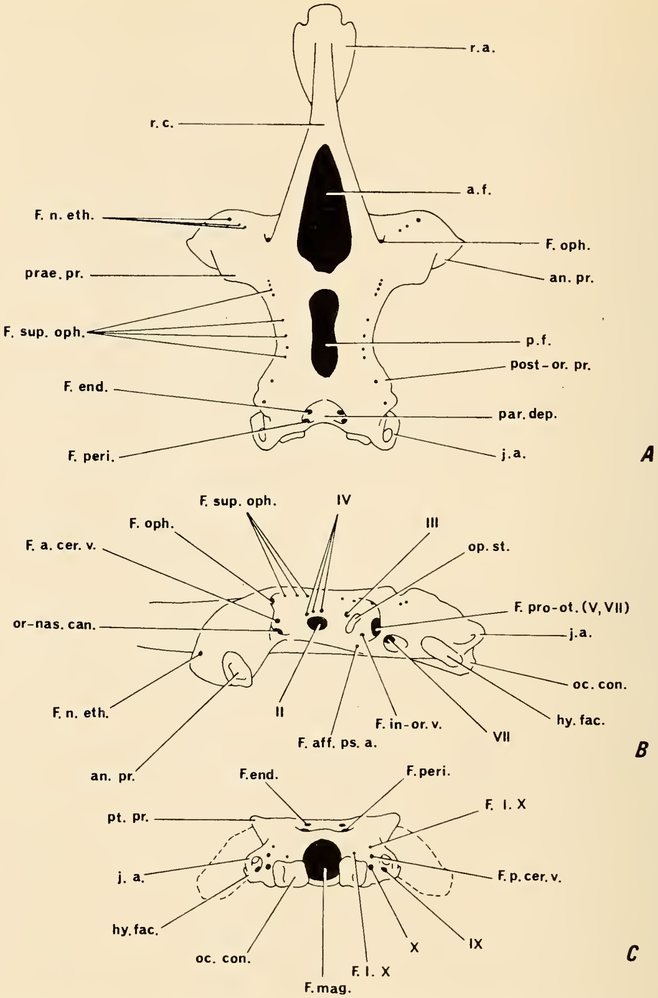

Fig. 48. Neurocranium of a typical rajid showing positions of foramina and fontanelles.

a.f.—anterior fontanelle; an.pr.—antorbital process; F.a.cer.v.—anterior cerebral vein foramen; F.aff.ps.a.—afferent pseudobranchial artery foramen; F.end.—endolymphatic foramen; F.in-or.v.—interorbital vein foramen; F.l. X—foramen of lateralis branch (X); F.mag.—foramen magnum; F.n.eth.—ethmoidal nerve foramen; F.oph—ophthalmic foramen; F.p.cer.v.—posterior cerebral vein foramen; F.peri.—perilymphatic foramen; F.pro-ot.—pro-otic foramen; F.sup.oph.—superficial ophthalmic foramen; hy.fac.—hyomandibular facet; j.a.—jugal arch; oc.con.—occipital condyle; or-nas.can.—oro-nasal canal; op.st.—optic stalk; p.f.—posterior fontanelle; par.dep.—parietal depression; prae.pr.—praeorbital process; post-or.pr.—postorbital process; pt.pr.—pterotic process; r.a.—rostral appendix; r.c.—rostral cartilage; II—optic nerve foramen; III—oculomotor nerve foramen; IV—pathetic (trochlear) nerve foramen; VII—foramen of hyomandibular branch (VII); IX—glossopharyngeal nerve foramen; X—vagus nerve foramen.

The nature of the bar and appendices have been described by Hulley (1970), while the varying lengths of the rostra in relation to cranial length are given in Table 2.

TABLE 2

Rostral length expressed as a percentage of the cranial length in southern African Rajidae.

Species	No. of specimens	Mean %
C. parcomaculata	3	39,6
C. triangularis	2	47,6
R. doutrei	2	63,5
R. pullopunctata	5	56,7
R. lanceorostrata	1	65,7
R. springeri	2	65,3
R. stenorhynchus	1	70,7
R. miraletus	5	45,6
R. clavata	10	48,1
R. straeleni	2	49,0
R. alba	4	57,0
R. radiata	2	46,2
R. robertsi	1	46,5
R. wallacei	2	45,4
R. caudaspinosa	6	37,6
R. leopardus	10	49,6
R. confundens	3	50,1
R. dissimilis	3	46,4
R. ravidula	3	52,4
R. spinacidermis	1	41,3
B. smithii	3	45,5

The course of the hypothetical line drawn from the tip of the rostrum and through the ophthalmic foramen to the occipital region, cuts the otic region in *Raja alba*, *R. leopardus* and *Cruriraja parcomaculata*, runs at a tangent to the otic region in *Raja doutrei* and *R. confundens*, and passes the otic region without touching in *Bathyraja smithii*, *Raja pullopunctata*, *R. clavata*, *R. miraletus*, *R. radiata* and *R. caudaspinosa*.

The nasal capsules are relatively thin-walled structures, which are attached to the side walls of the brain case. They are orientated to form a right angle with the median axis of the cranium in *Rhinobatos halavi* (El-Tourbi & Hamdy 1959: pl. 1), *Bathyraja smithii*, *Raja clavata*, *R. straeleni*, *R. caudaspinosa*, *R. confundens* and *Cruriraja parcomaculata* (Figs 49 A, E; 51 A, D; 53 A, E). The angle is slightly acute in *Raja stenorhynchus*, *R. springeri*, *R. lanceorostrata*, *R. doutrei*, *R. pullopunctata*, *R. miraletus*, *R. radiata*, *R. robertsi*, *R. dissimilis*, *R. ravidula* and *R. leopardus* (Figs 50 A, D, E, F, G; 51 E; 52 D, E; 53 D; 54 A, D), more so in *R. wallacei* (Fig. 54 F), and extremely acute in *R. alba* and *R. spinacidermis* (Figs 52 A; 54 E). In *Raja spinacidermis*, *R. ravidula*, *R. dissimilis* and *R. robertsi* (Figs 52 D; 53 D; 54 D, E), the nasal capsules are comparatively larger than in the other species. There is a well-developed articular process for the attachment of the antorbital process at the latero-posterior edge of each nasal capsule, while antero-dorsally there is usually one small foramen (sometimes more, e.g. *Raja clavata* (Fig. 51 A))

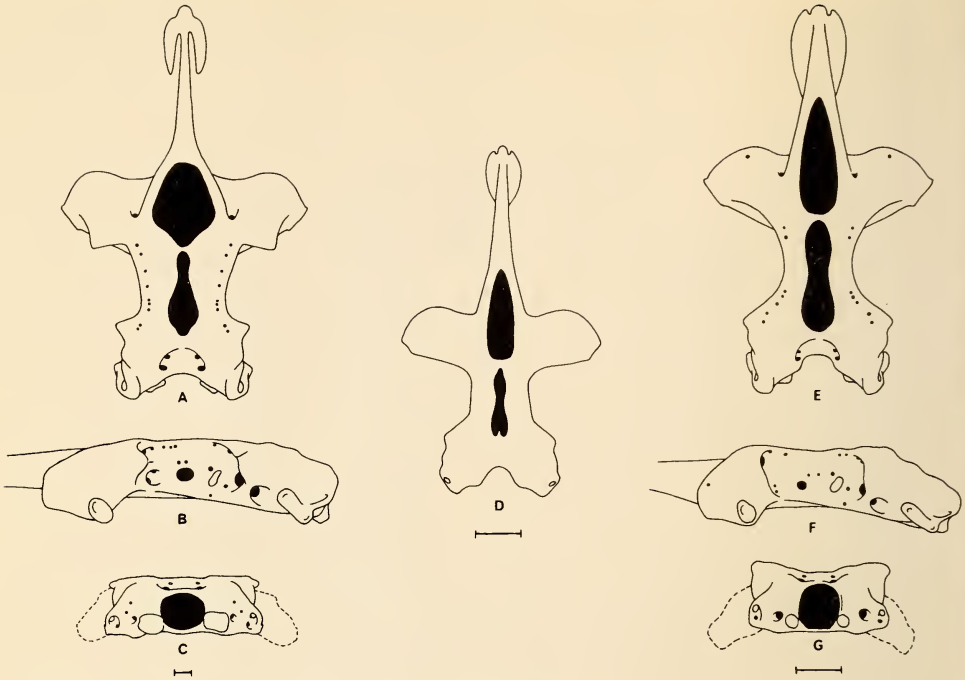

Fig. 49. Dorsal, lateral and posterior views of the neurocrania of:
A. B. C. *Bathyraja smithii*; D. *Cruriraja triangularis* (X-ray reconstruction); E. F. G. *C. parcomaculata*.

for the passage of the ethmoidal nerve, a small, lateral branch of the superficial ophthalmic nerve. The foramen appears to be absent in *Bathyraja smithii*, *Raja leopardus* and *R. confundens* (Figs 49 A; 53 A; 54 A). However, the close proximity of this foramen to the ophthalmic foramen in *Raja caudaspinosa* (Fig. 53 E) suggests that the ethmoidal nerve and the superficial ophthalmic nerve may have a common foramen in these species.

The *crista supraorbitalis* is continued anteriorly to expand on the postero-dorsal region of the nasal capsule, where it develops to form the preorbital process (*crista praeorbitalis* of Heintz (1962); preorbital cartilage of Holmgren (1940)). The preorbital process is best developed in *Rhinobatos halavi* (El-Tourbi & Hamdy 1959: pl. I A), *Bathyraja smithii*, *Raja clavata*, *R. miraletus* and *R. alba* (Figs 49 A; 51 A, E; 52 A), not so marked in *Raja doutrei*, *R. pullopunctata*, *R. radiata*, *R. leopardus*, *R. confundens* and *R. caudaspinosa* (Figs 50 A, G; 52 E; 53 A, E; 54 A), and least developed in *Cruriraja parcomaculata* (Fig. 49 E).

The *crista supraorbitalis*, which forms the dorsal border of the orbit, is perforated by a series of small foramina for the superficial ophthalmic nerves. The number of foramina varies in specimens of the same species and may even vary on opposite sides of the same specimen. The orbital region is characterized by the anterior position of the optic foramen, which is typical of the Rhinobatidae (El-Tourbi & Hamdy 1959) as well as of rajids (Figs 49–54). The optic

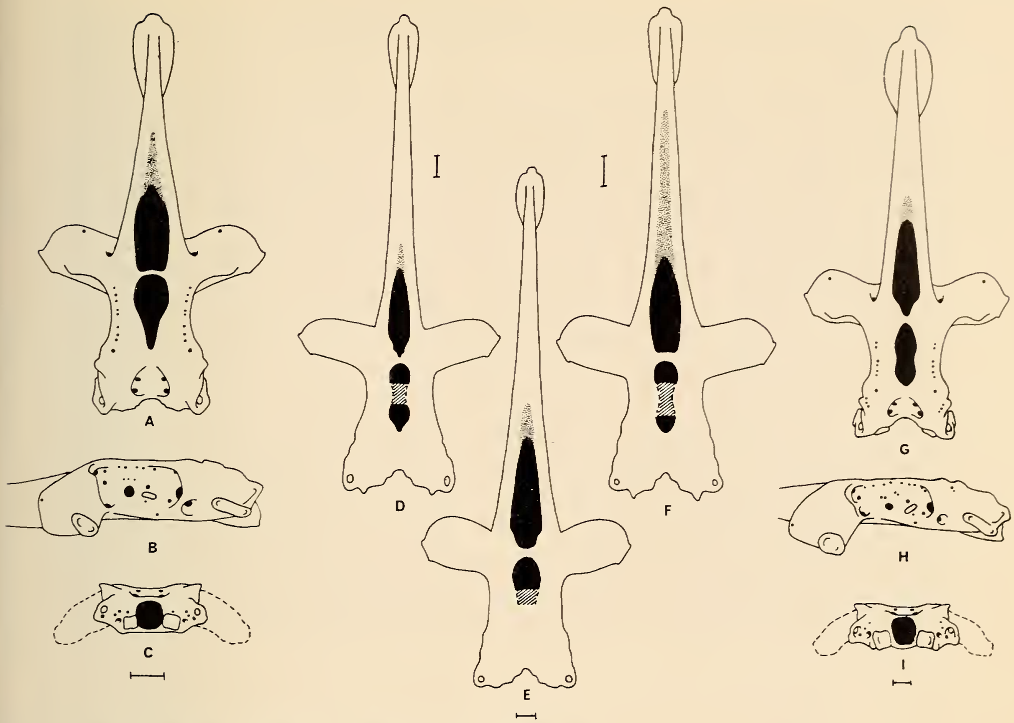

Fig. 50. Dorsal, lateral and posterior views of the neurocrania of:
A. B. C. *Raja pullopunctata*; D. *R. lanceorostrata* (X-ray reconstruction); E. *R. stenorhynchus* (X-ray reconstruction); F. *R. springeri* (X-ray reconstruction); G. H. I. *R. doutrei*.

foramen appears to be somewhat more anteriorly positioned in *Raja radiata*, *R. confundens*, *R. leopardus* and *R. caudaspinosa* (Figs 52 F; 53 B, F; 54 B) than it is in the other species. Above the optic foramen are a series of two or three small foramina for the passage of the pathetic (trochlear) nerve, the most anterior of which is the largest. Although these branches of the pathetic all innervate the superior oblique muscle, the single, large foramen, typical of *Rhinobatos* (Daniel 1934; El-Tourbi & Hamdy 1959) has not been found in rajids. The position of the pathetic foramen given by Heintz (1962) is erroneous and has obviously been confused with the foramen for the anterior cerebral vein.

In the antero-ventral region of the orbit is the large orbito-nasal canal foramen, which runs into the nasal capsule and accommodates the anterior facial vein (Holmgren 1940; El-Tourbi & Hamdy 1959). In *Cruriraja parcomaculata* (Fig. 49 F), the orbito-nasal canal is much narrower. Hyman (1942) points out that in the skate, the deep ophthalmic nerve leaves the orbit via the orbito-nasal canal, but dissection of several species has revealed that this nerve joins the superficial ophthalmic nerve at the antero-dorsal region of the orbit, the two nerves passing through a single foramen, the ophthalmic foramen. This is also found in *Rhinobatos halavi*, *Rhynchobatos djiddensis* and *Trygon kuhlii*

(El-Tourbi & Hamdy 1959) and would therefore appear to be a constant feature in batoids.

Between the ophthalmic foramen and the foramen for the orbito-nasal canal is a small foramen for the passage of the anterior cerebral vein. In *Bathyraja smithii*, *Raja miraletus* and *R. clavata* (Figs 49 B; 51 B, F), it is situated at about the same level as the optic foramen, in *Raja alba* (Fig. 52 B) it is displaced ventrally, and in *Raja doutrei*, *R. pullopunctata*, *R. radiata*, *R. confundens*, *R. leopardus* and *R. caudaspinosa* (Figs 50 B, H; 52 F; 53 B, F; 54 B) it is displaced dorsally.

Posterior to, and at about the same level as, the optic foramen is the cartilaginous optic stalk, above which is a single foramen for the oculomotor (III) nerve. The most conspicuous foramen in the orbit is the large pro-otic foramen, which is separated from the smaller foramen of the hyomandibular branch (VII) by the prefacial commissure. Positioned anteriorly to the prefacial commissure and almost at the ventral edge of the orbit is a very small foramen for the afferent pseudobranchial artery. Between this and the pro-otic foramen is another small aperture for the interorbital vein (pituitary vein of El-Tourbi & Hamdy (1959)), which runs into the cranial cavity in the *sella turcica*, placing the two orbits in communication with one another. This has been incorrectly termed the abducent foramen by Heintz (1962), although it has been labelled as IV (trochlear) in the figure (fig. 2 B). Dissection has revealed that, as in the

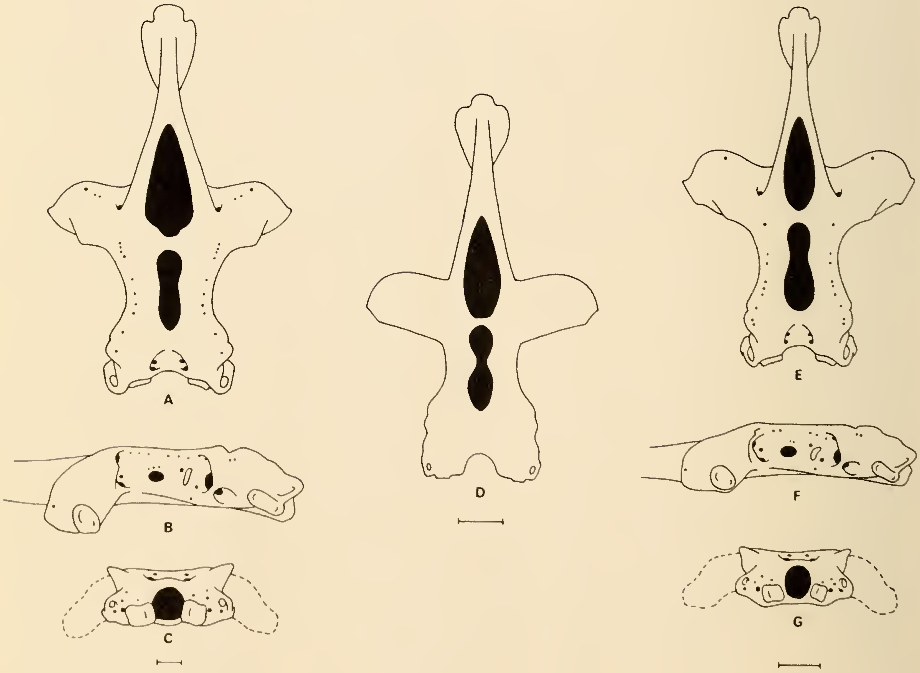

Fig. 51. Dorsal, lateral and posterior views of the neurocrania of:
A. B. C. *Raja clavata*; D. *R. straeleni* (X-ray reconstruction); E. F. G. *R. miraletus*.

case of *Rhinobatos halavi*, *Rhynchobatos djiddensis* and *Trygon kuhlii* (El-Tourbi & Hamdy 1959), the abducent nerve enters the orbit through the pro-otic foramen in rajids.

The posterior border of the orbital region is marked dorsally by the small postorbital process. It is most prominent in *Bathyraja smithii* (Fig. 49 A). On each side of the neurocranium, at its posterior end, are the auditory capsules, between which is the parietal depression (endolymphatic fossa of El-Tourbi & Hamdy (1959)). This is similarly situated in all rajid species and contains two pairs of foramina leading to the auditory capsules. The anterior pair are the endolymphatic foramina and the posterior pair, which lead directly to the perilymphatic cavity, are the perilymphatic foramina.

At the posterior edge of the lateral surface of the auditory capsule is the articular facet of the hyomandibular cartilage, which is in the form of an elongate, slightly concave groove, running antero-dorsally. It is bordered dorsally by a shallow depression, the postorbital groove, which contains the posterior region of the postorbital sinus. This vessel passes through the jugal arch to become the anterior cardinal vein (jugular vein of Heintz (1962)) at the junction with the posterior cerebral vein (O'Donoghue & Abbott 1928). The jugal arch links the protuberance of the hyomandibular facet to the posterior region of the auditory capsule. Its size and position (Figs 49–54) seem to bear

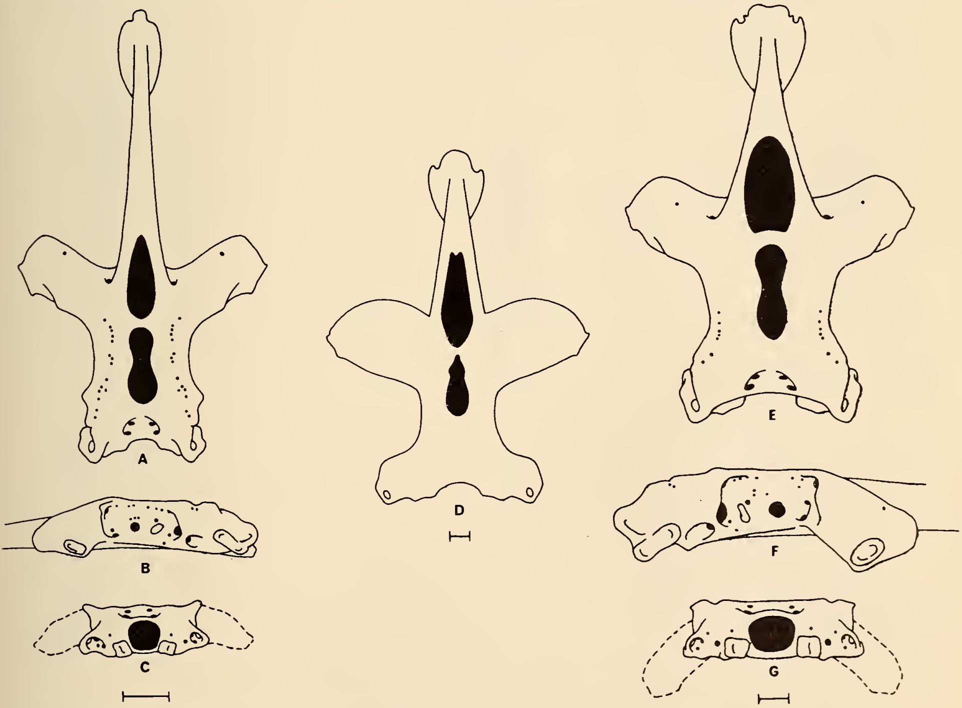

Fig. 52. Dorsal, lateral and posterior views of the neurocrania of:
A. B. C. *Raja alba*; D. *R. robertsi* (X-ray reconstruction); E. F. G. *R. radiata*.

some relationship to the groupings suggested by the clasper structure.

The occipital region of the neurocranium is more or less similar in form in all species (Figs 49–54), although the skull appears to be comparatively higher and narrower in *Raja confundens* and *R. caudaspinosa* (Figs 53 C, G). Foramina for the posterior cerebral vein are absent in *Cruriraja parcomaculata* (Fig. 49 G), so that in this species the vein probably leaves the cranial cavity together with the vagus nerve (X), as in the case of *Squalus acanthias* (O'Donoghue & Abbott 1928).

The ventral surface of the neurocranium runs forwards from the occipital region as a flat plate, although it forms a shallow subethmoidal depression between the bases of the nasal capsules. Medially, it is perforated by one (sometimes two) small foramen, through which the internal carotid artery enters the cranial cavity. Hyrtl (1872) has described the cross-over system of the internal carotids in *Raja clavata*. Anterior to the subethmoidal depression, the prolongation of the trabecular plates leads to the formation of the rostral cartilage (El-Tourbi & Hamdy 1959), which runs in an even curve towards the tip of the snout. As has been pointed out (Hulley 1970: fig. 20), some lateral undulation of the rostral cartilage occurs in *Bathyraja smithii*, but dorsal/ventral undulation of the rostral cartilage, especially at its anterior extremity, is found

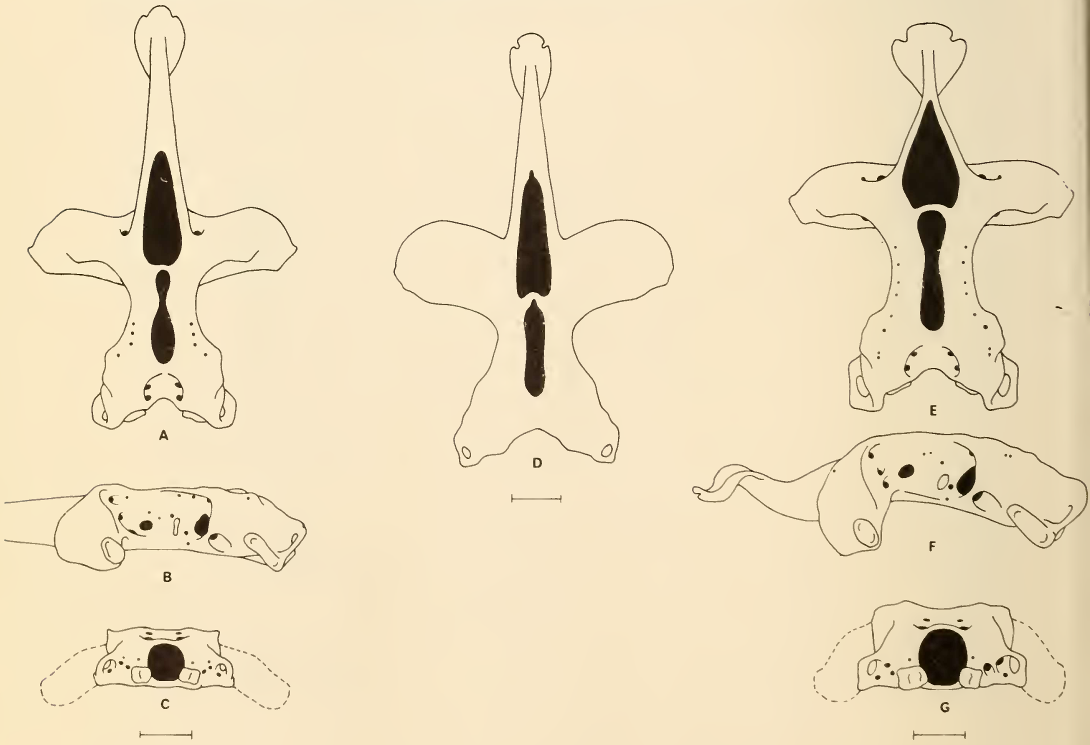

Fig. 53. Dorsal, lateral and posterior views of the neurocrania of:
A. B. C. *Raja confundens*; D. *R. dissimilis* (X-ray reconstruction); E. F. G. *R. caudaspinosa*.

only in *Raja caudaspinosa* (Fig. 53 F).

The dorsal surface of the neurocranium is perforated by two large fontanelles, separated by the narrow epiphysial bridge. The most anterior of these, usually termed the anterior fontanelle, is an amalgamation of the precerebral fontanelle and the anterior supracranial fontanelle (Hamdy 1960). The posterior fontanelle should therefore be correctly termed the posterior supracranial fontanelle (El-Tourbi & Hamdy 1959; Hamdy 1960). In *Rhinobatos halavi* and *Rhinobatos productus* (Daniel 1934: fig. 62), the anterior fontanelle is moderately wide at its posterior end, and narrows anteriorly to run as a groove, almost to the tip of the rostral cartilage, i.e. there is no marked anterior border to the fontanelle in these species. Anterior grooving of the rostral cartilage is found only in *Raja doutrei*, *R. pullopunctata*, *R. lanceorostrata* and *R. stenorhynchus* (Fig. 50) and reaches its maximum development in *R. springeri* (Fig. 50 F). In these species the posterior region of the anterior fontanelle is moderately wide, while the posterior margin is produced in *Raja doutrei* and *R. lanceorostrata* (Figs 50 D, G), and evenly curved in *Raja pullopunctata*, *R. stenorhynchus* and *R. springeri* (Figs 50 A, E, F). In *Bathyraja smithii* (Fig. 49 A) the anterior fontanelle is pear-shaped, with a broad posterior region and an evenly curved anterior margin, which is not elongated to form a furrow. In *Raja clavata*,

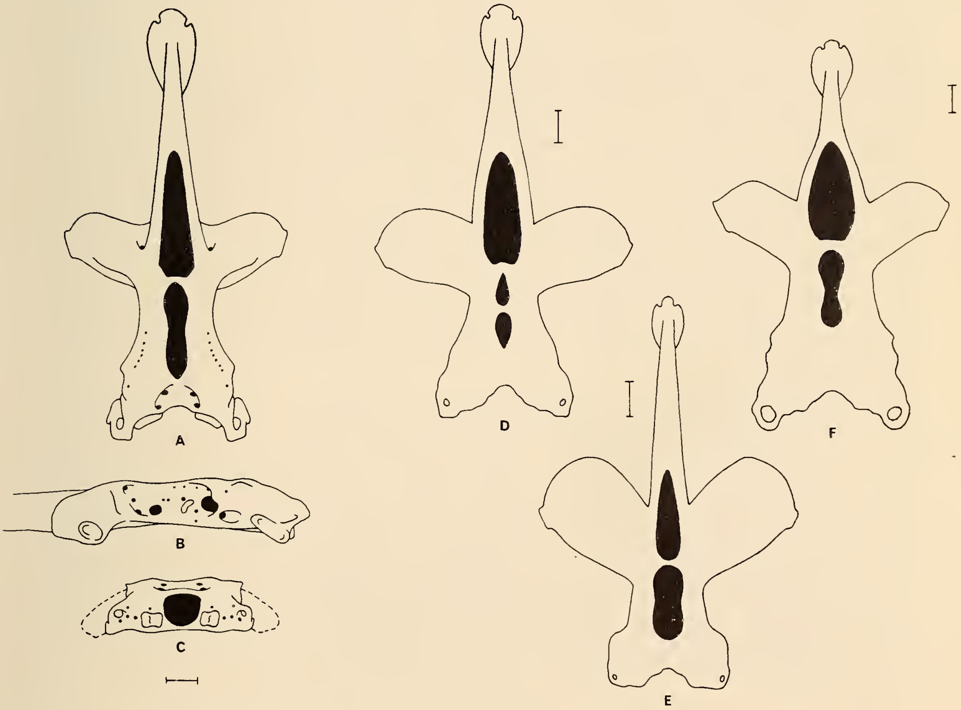

Fig. 54. Dorsal, lateral and posterior views of the neurocrania of:
A. B. C. *Raja leopardus*; D. *R. ravidula* (X-ray reconstruction); E. *R. spinacidermis* (X-ray reconstruction); F. *R. wallacei* (X-ray reconstruction).

R. straeleni, *R. miraletus*, *R. alba* and *R. wallacei* (Figs 51 A, D, E; 52 A; 54 F) the fontanelle is moderately obovate, while in *Raja dissimilis*, *R. ravidula*, *R. confundens* and *R. leopardus* (Figs 53 A, D; 54 A, D) it is narrowly obovate, with a convex posterior margin. In *Raja radiata* (Fig. 52 E) it is broadly obovate, and in *R. robertsi* (Fig. 52 D) ellipsoid with a truncate anterior margin. The fontanelle in *Raja spinacidermis* (Fig. 54 E) is reduced and extends only for about one-third the length of the rostral cartilage, but in *Raja caudaspinosa*, and *Cruriraja parcomaculata* (Figs 49 E; 53 E) it is broadly obovate and reaches the level of the rostral appendices. *Cruriraja triangularis* (Fig. 49 D) differs from *C. parcomaculata* in that the anterior fontanelle does not reach the level of the rostral appendices.

The posterior fontanelle is difficult to follow, especially in X-ray photographs, but it appears to be more or less similar in all species, being constricted to form a waist medially. This does not appear to be the case in *Raja pullopunctata* and *R. dissimilis* (Figs 50 A; 53 D), while in *R. ravidula* (Fig. 54 D) two posterior fontanelles are present. The extent of the posterior fontanelles, their anterior and posterior margins, and the degree of constriction vary in the different species (Figs 49–54).

Discussion

It is recognized (Bigelow & Schroeder 1962) that the suborder Rajoidea may be divided into four families, Rajidae, Arhynchobatidae, Pseudorajidae and Anacanthobatidae, on the basis of the number of dorsal fins and the nature of the anterior lobe of the pelvic fin. De Buen (1959) recognized a further family Gurgesiellidae, based on a single specimen (*Gurgesiella furvescens*) from the abyssal region off Valparaiso, Chile. However, Bigelow & Schroeder (1962) hold that the characters on which the family were based appear to fall within the Pseudorajidae and have synonymized the two. It is now apparent that, not only is the family Gurgesiellidae valid, but also that *Pseudoraja atlantica*, known from the Atlantic coast of Nicaragua, falls within this family (Hulley 1972). It appears that the Rajidae possess common, but distinguishable characters in the structure of the pelvic bar and in the number of proximal basal segments in the myxopterygia.

As has been pointed out, two intermediate segments connect the basipterygium with the axial cartilage in *Raja*, *Cruriraja*, *Bathyraja* and *Anacanthobatis*. This would support the view that the number of basal segments varies within large groups of elasmobranchs (Huber 1901), and cannot be used for the separation of families within the Rajoidea. In terms of the pelvic girdle, the basic plan of a transverse (or only slightly arched) pelvic bar, with a pair of lateral prepelvic processes, is adhered to in the Rajoidea. However, the girdles can be divided into four (six, with the inclusion of the Pseudorajidae and Gurgesiellidae) distinctive groups.

Group 1

Pelvic bar simply transverse; lateral prepelvic processes of varying length; iliac processes recurved; two or more obturatorial foramina.

The prepelvic processes appear to vary considerably in length between closely related species, e.g. *Raja clavata* and *R. straeleni* (Figs 3 g, j), so that this does not appear to be a suitable diagnostic character within the group. On the basis of anterior arching of the bar, the black-bellied skates may be recognized as a separate, identifiable subgroup. In the remaining species, there appears to be a gradation in the recurvature of the iliac processes, with *Bathyraja smithii* and *Raja spinacidermis* representing the two limits of the sequence (Fig. 3).

Group 2

Pelvic girdle transverse, with iliac region poorly developed; single obturatorial foramen.

This group includes the monotypic genus *Arhynchobatis*, known only from New Zealand.

Group 3

Pelvic girdle simply transverse, with iliac regions moderately developed; one obturatorial foramen; prepelvic processes poorly developed; iliac processes large and recurved.

This group includes all species of the genus *Cruriraja* from South Africa, as well as *C. rugosa* from the Gulf of Mexico.

Group 4

Pelvic girdle transverse, with iliac regions greatly developed; single large obturatorial foramen; iliac processes small; prepelvic processes large.

This group includes both the South African and North American representatives of the family Anacanthobatidae.

The present taxonomy recognizes that groups 1, 2 and 4 form separate families within the Rajoidea, namely Rajidae, Arhynchobatidae and Anacanthobatidae respectively, while group 3 (*Cruriraja*) is considered to be a genus within the Rajidae. However, it is now proposed that, on the basis of the pelvic girdle, a new family Crurirajidae be erected to contain the genus *Cruriraja*. This is further supported by the structure of the clasper. The family will be defined at a later stage in this paper. Similarly, on the basis of the structure of the pelvic girdle, neurocranium and hyomandibular cartilage, the Gurgesiellidae and Pseudorajidae are now recognized to be distinct families (Hulley 1972). Examination of the X-ray photographs of *Psammobatis lima*, *P. scobina*, *P. extenta* and *P. microps* has revealed that the girdles are not unlike those of *Raja clavata* and *R. miraletus* (Figs 3 i, j) and would therefore not necessitate the recognition of a further family at this stage. However, detailed studies of the structure of the claspers of these species is required.

The southern African Rajidae can be grouped into eight distinguishable types, on the basis of the clasper structure:

TYPE A: *Bathyraja smithii* (Müller & Henle).

Claspers very slender and elongate, with club-shaped distal glans; well-developed pseudosiphon on outer dorsal wall; internally, shield and spike absent, but sharp-edged knife lying beneath projection; rhipidion absent, pseudorhipidion present; dorsal terminal 3 situated laterally to dorsal terminal 2; ventral terminal simple.

Although the single species was referred to the genus *Bathyraja* because of the structure of the rostral bar and appendices (Hulley 1970), there is no doubt that this type of clasper is characteristic of the genus (Ishiyama 1958; Ishiyama & Hubbs 1968; Stehmann 1970). However, Ishiyama & Hubbs (1968) have given diagnostic characters, which are not altogether correct for the genus (Hulley 1970). The pseudorhipidion and pseudosiphon are not wholly confined to the genus: the former is found in *Raja clavata*, *R. straeleni*, *R. miraletus* and *R. alba* (in *Bathyraja smithii* (Hulley 1970: fig. 21), the pseudorhipidion is not labelled, although the associated dorsal marginal cartilage is well developed (Fig. 29)); the latter is present in *Raja radiata*, *R. robertsi* and possibly in *R. wallacei* and *R. caudaspinosa*. Differences based on distribution for the separation of *Bathyraja* from *Breviraja* given by Ishiyama & Hubbs (1968) add to the confusion, and it is now considered that *Bathyraja* is a bipolar, antitropical genus, while *Breviraja* is confined to slope areas in the tropics (Hulley 1970).

In terms of clasper structure, the Japanese subgenus *Rhinoraja* can be separated from *Bathyraja* by its distinct, external pseudosiphon, large dorsal terminal 1 cartilage and elongate ventral marginal cartilage. However, these characters do not seem to be that significant, for a distinct external pseudosiphon is present in *Bathyraja matsubarai*, *B. aleutica* and *B. diplotaenia* (Ishiyama 1958: fig. 3), the dorsal terminal 1 is not markedly reduced in some *Bathyraja* species (Ishiyama 1958: fig. 8), and the ventral marginal is particularly elongate in *Bathyraja trachouros* and *B. abasiriensis*. The subgenus *Rhinoraja* can therefore be distinguished only on the segmented nature of the rostral bar.

It should be noted that the shape of the accessory terminal cartilage in *Bathyraja smithii* (Fig. 24 a) is very similar to that in *Rhinoraja odai* and *Rhinoraja longicauda* (Ishiyama 1958: fig. 11). However, the nature of the rostral bar precludes its identification within the genus *Rhinoraja*.

Type A corresponds to Stehmann's *spinicauda*-type, which includes *Bathyraja spinicauda*, *B. pallida* and *B. richardsoni* (with reservation), and which is now held to be equivalent to the genus *Bathyraja* (Stehmann 1970).

TYPE B. *Raja doutrei* Cadenat; *R. pullopunctata* Smith; *R. lanceorostrata* Wallace; (and probably includes *R. springeri* Wallace and *R. stenorhynchus* Wallace).

Clasper moderately long, naked, with spatulate distal tip more or less dorso-ventrally flattened; pseudosiphon absent; inner dorsal lobe of glans with two clefts, separated by terminal bridge; rhipidion well developed; shield large and covered with pleated epithelia; sentinel usually small and bluntly rounded or absent; spike always present, sometimes hooked; ventral terminal with dorsally convex, outer lateral margin; accessory terminal 1 with asymmetrical, proximal arms; accessory terminal 2 with or without attachment process.

All southern African 'black-bellied' skates are included in this group, which is comparable with the *oxyrhynchus*-group of the eastern North Atlantic (Stehmann 1969, 1970). The group apparently has a world-wide distribution with the following species: *Raja batis*, *R. oxyrhynchus* and *R. nidarosiensis* in the eastern North Atlantic; *Raja laevis*, *R. oregoni*, *R. bullisi*, *R. floridana* and *R. garricki* in the western North Atlantic; *R. flavirostris* in the western South Atlantic; *Raja rhina* and *R. binoculata* in the eastern North Pacific; *Raja australis*, *R. nasuta* and possibly *Zearaja gudgeri* around Australia and New Zealand; and the species of the subgenus *Tengujei* Ishiyama (*Raja tengu*, *R. pulchra*, *R. macrocauda* and *R. gigas*) in the western North Pacific. These species inhabit the continental shelf area and penetrate the slope regions to between 350 m and 550 m, with a maximum recorded depth of 740 m in the case of *Raja springeri* (Wallace 1967).

The poor degree of development of the distal projection of the accessory terminal 1 appears to be characteristic of all the species, so that the sentinel is poorly developed in the glans. Of the species examined, Ishiyama (1958) reports a massive development of the accessory terminal 1 cartilage in a single species, *Raja pulchra*, where the condition of the cartilage (Ishiyama 1958: fig. 16; 1967: fig. 9) approximates to the condition found in *Raja clavata* and *R. straeleni*. However, there are marked dissimilarities in the detachment process and in the accessory terminal 2 cartilage between *Raja pulchra* and *R. clavata* and *R. straeleni*.

Raja pullopunctata does not possess a sentinel in the glans, as the distal projection of the accessory terminal 1 does not develop (Fig. 24 d).

A well-developed and hooked spine is found in *Raja lanceorostrata* and in the Japanese species *R. gigas* (Ishiyama 1958, 1967) and further similarities are shown in the parallelogram-shaped dorsal terminal 1 and the distal projection of the dorsal marginal cartilage (Fig. 31; Ishiyama 1967: fig. 11). However, differences can be seen in the dorsal terminal 2 and 3 cartilages, the proximal elongation of the outer edge of the dorsal terminal 1 cartilage, the expansion of the distal projection of the accessory terminal 1 and the attachment process of the accessory terminal 2. Furthermore, the outer lateral edge of the ventral terminal appears to be comparatively broader in *Raja gigas*.

The spatulate terminal end to the distal projection of the accessory terminal 1 is found in *Raja lanceorostrata* (Fig. 24 c), *R. batis* (Hulley 1966: fig. 7) and *R. garricki*, but there are marked differences in the structure of the dorsal terminal 1, ventral terminal and accessory terminal 2 cartilages between the species. The degree of hooking of the accessory terminal 2 in the geographically separated species *Raja batis*, *R. lanceorostrata*, *R. macrocauda*, *R. gigas* and *R. garricki* may be considered in terms of parallel evolution.

The possession of an anteriorly arched pelvic bar is peculiar to the southern African species of 'black-bellied' skate (see above) and in the South American species *Raja flavirostris* (Fig. 3 f) and has been confirmed in the case of *R. garricki* and *R. oregoni* from the western North Atlantic. It would appear, therefore, that this condition of the pelvic bar is characteristic of the group as a whole.

'Black-bellied' skates were recognized as a separate group, *Gammaraia*, by Leigh-Sharpe (1925), who proposed the pseudogenus on the basis of external clasper structure. However, this taxon has no nomenclatural standing (Jordan

1925; Bigelow & Schroeder 1953). On the other hand, Ishiyama (1958) identified the Japanese representatives of the group as a separate subgenus, *Tengujei*. Stehmann (1969) has reviewed the taxonomic validity of Ishiyama's subgenus, and proposed that the name *Laeviraja* Bonaparte, 1838 (type-species *Raja oxyrhynchus*) be employed. It appears, however, and has been confirmed (Stehmann 1970), that the name *Dipturus* Rafinesque, 1810 (type-species *Raja batis*) has priority.

TYPE C: *Raja clavata* Linnaeus; *R. straeleni* Poll; *R. miraletus* Linnaeus.

> Claspers moderately long, with naked outer surface; some species with pecten on outer dorsal lobe; pseudosiphon absent, but inner dorsal lobe with pocket and cleft; sentinel massively developed, with knife-edged outer lateral margin, fitting into pocket; spike situated distally in sentina; fleshy signal situated proximally at about level of well-developed pseudorhipidion; ventral terminal characteristically J-shaped, with distal protuberance, forming funnel.

Hulley (1970) has pointed out that the species *Raja clavata*, *R. straeleni*, *R. herwigi* and *R. maderensis* form a complex of very closely related species within the genus *Raja*. It would appear that the species *Raja miraletus* can now be identified with the complex. Stehmann (1970) terms this complex the *clavata*-group, and considers it to be a separate subgenus *Raja* Linnaeus (type-species *Raja miraletus*).

Stehmann (1969: 137) is of the opinion that the species *Raja picta* and *R. alba* are members of the subgenus, although they represent 'slightly divergent forms'. This may be true in the case of *Raja picta*, where, although there appear to be marked differences in the structure of the ventral terminal and accessory terminal 2 cartilages, some similarities are shown by the dorsal terminal 1 and 2 cartilages. Furthermore, *Raja picta* possesses a signal. However, *Raja alba* should be considered as a separate subgenus. It will be defined at a later stage.

It has been pointed out (Hulley 1970) that *Raja straeleni* closely resembles *R. clavata*, but that the two were held to be distinct on the basis of colour pattern and of differences in the shield of the clasper glans. There are further differences in the clasper cartilages of the two species. In *Raja straeleni*, the dorsal terminal 1 is narrower and more blunt distally (Figs 16 g, h), the accessory terminal 2 is comparatively broader and distally more pointed (Figs 26 e, f), and the outer lateral margin of the ventral terminal is better developed (Figs 22 e, f). The most marked difference occurs in the dorsal terminal 2 (Figs 18 e, f), which in *Raja straeleni* possesses numerous, small, blunt processes on its outer lateral wall. While the clasper cartilages are species specific without exception (Ishiyama 1958), the differences between *Raja clavata* and *R. straeleni* appear to be minor, suggesting that *R. straeleni* could be regarded as a subspecies of *R. clavata*. Recently, Stehmann (1971*b*) has re-examined this question, and concludes that the species are distinct.

The subgenus *Raja* appears to be confined to shelf areas of the eastern North Atlantic and eastern South Atlantic (Stehmann 1970), with a bipolar distribution pattern shown by the species *Raja clavata* (Hulley 1966). *Raja* *miraletus* is now known to extend into the south-western Indian Ocean (Hulley 1969) and has been reported from the Kerala coast in India (Samuel 1963).

TYPE D: *Raja alba* Lacépède.

Clasper massive, with pecten on outer dorsal surface, but without pseudosiphon; pseudorhipidion well developed; inner dorsal lobe with proximal cleft, but without distal slit or pocket; shield prominent with laminate integument; sentinel massive and situated far distally; spike and signal absent; four dorsal terminal cartilages, with pecten developed from outer lateral margin of dorsal terminal 3; ventral terminal with dorsally convex, wide, outer lateral margin.

While Leigh-Sharpe (1924) considered that *Raja alba* belonged to a separate pseudogenus *Iotaraia*, Stehmann (1969: 136) pointed out that *R. alba* is closely related to the *clavata*-group, although 'in etwas abweichender Richtung entwickelte Formen gelten'. It now appears obvious from the examination of the number and arrangement of the internal cartilages that Leigh-Sharpe's supposition was correct, but his pseudogenus has no taxonomic standing (Jordan 1925; Bigelow & Schroeder 1953).

Firstly, there are four dorsal terminals in *Raja alba*, which are arranged so that they extend distally from the dorsal marginal to the axial tip, so forming the framework of the dorsal lobe (Fig. 33). In this arrangement, *Raja alba* approximates to *Raja radiata*, *R. caudaspinosa*, *R. dissimilis*, *R. confundens*, *R. leopardus* and *R. wallacei*. In the subgenus *Raja*, there are only two dorsal terminal cartilages and the connection between these and the axial tip is formed from connective tissue only. Secondly, *Raja alba* lacks the accessory terminal 3 and 4 cartilages (forming the signal) which are characteristic of the subgenus *Raja*.

It would appear that parallel evolution has occurred in the formation of the pecten, which presumably acts as a holdfast structure. However, as has been pointed out above, the pecten in *Raja miraletus* (subgenus *Raja*) is formed from the dorsal terminal 2, while in *Raja alba*, it is formed by the dorsal terminal 3 cartilage.

Leigh-Sharpe's (1924) classification of *Raja alba* (= *Raja marginata* Lacépède) in the pseudogenus *Iotaraia* has no taxonomic standing. A new subgenus, *Rostroraja*, is therefore proposed to include the species *Raja alba*, and is defined on page 77. The subgenus shows bipolar distribution patterns in the eastern Atlantic (Hulley 1966: fig. 8) and is reported to extend as far north as off Barra Falsa, Moçambique, in the Indian Ocean (Wallace 1967). It inhabits shelf areas from 50 m to 360 m.

Although the following groups are held to be equivalent to their European counterparts, there are differences in the interpretation of the number of dorsal terminal cartilages and in the shape of the axial cartilage.

Stehmann (1969, 1970) considers that in the *fullonica*-type (subgenus *Leucoraja*), *radiata*-type (subgenus *Amblyraja*) and *fyllae*-type (subgenus *Rajella*), the axial is completely recurved on itself, so that it attains a marked J-shape. In *Amblyraja* and *Rajella*, the recurved tip of the axial then connects with a small dorsal terminal 4 cartilage, to form the framework of the dorsal lobe, while in *Leucoraja*, which has a similarly recurved axial, this cartilage connects directly with the external surface of the dorsal terminal 3. In this subgenus, a dorsal terminal 4 is absent.

These interpretations are now held to be incorrect. It has been found that in the species *Raja dissimilis*, *R. confundens*, *R. caudaspinosa* and *R. leopardus* (Figs 36–39) a dorsal terminal 4 cartilage is present, and consists of a flattened, slightly dorsally convex plate, which runs from the external surface of the dorsal terminal 3 to the axial tip. In these species the cartilage is heavily calcified and well demarcated, both from the axial and from the dorsal terminal 3 cartilages. The axial in these cases is therefore spatulate or only very slightly recurved, and is somewhat similar to the condition of the cartilage in Japanese rajids of the southern form (Ishiyama 1958). In Type E (*Raja radiata*: subgenus *Amblyraja* of Stehmann) the dorsal terminal 4 is not heavily calcified, so that its texture resembles that of the axial. It is held that Stehmann (1969, 1970) has incorrectly termed the calcified proximal end as the dorsal terminal 4 and has referred the distal end to the axial. In *Raja fullonica*, *R. circularis* and *R. naevus* (subgenus *Leucoraja*), Stehmann (1969, 1970) finds no dorsal terminal 4 cartilage, but in the southern African species *Raja wallacei* (Fig. 35), which is obviously of the same subgenus, a dorsal terminal 4 cartilage, which is usually well calcified, is easily identifiable. Therefore, the axial cartilage is spatulate or only slightly recurved. Furthermore, the subgenera *Amblyraja*, *Leucoraja* and *Rajella* show an obvious sequence, especially in regard to the dorsal terminal 3 cartilage, when considered in the light of these findings.

TYPE E: *Raja radiata* Donovan; *R. robertsi* Hulley.

Claspers short and club-like; pseudosiphon in outer dorsal lobe; spur well developed, forming outer border of distal cleft; sentinel partly covering spike; pent extending distally from rhipidion; distal end of prominent shield with laminate integument; four dorsal terminal cartilages; ventral terminal typically J-shaped; accessory terminal 1 characteristic, with concave dorsal surface, enveloping the accessory terminal 2.

The pseudogenus *Deltaraia* was proposed by Leigh-Sharpe (1924) to include the species *Raja radiata* and *R. naevus*. However, Stehmann (1970) has grouped the species *Raja radiata* and *R. hypoborea* as a separate subgenus, *Amblyraja* Malm, 1877, and, mainly on the basis of clasper structure, has shown that *Raja naevus* should be referred to the subgenus *Leucoraja* Malm, 1877.

From its morphometry and the presence of a pseudosiphon in the claspers of the juvenile male type, Hulley (1970) has suggested that *Raja robertsi* should be included with *R. radiata*, so forming a group which encompasses the species *Raja duellojuradoi*, *R. frerischi* and *R. georgiana* in the western South Atlantic, *R. jenseni* from the western North Atlantic and *R. badia* from the Gulf of Panama. The bipolar distributional pattern of the twin species has already been pointed out (Krefft 1968*b*). All species of this subgenus inhabit slope areas of the archibenthal and some penetrate to abyssal depths. It should be pointed out that *Raja badia* is at present the only species of the subgenus not found in the Atlantic.

TYPE F: *Raja wallacei* Hulley.

Claspers short and spatulate; dermal denticles usually present externally; cavity in musculature of outer dorsal lobe usually present (? pseudosiphon); proximal slit bordered by roll; distal cleft bordered by small spur, usually covered by integument; promontory present; spike and sentinel small and situated far distally; rhipidion fan-shaped; four dorsal terminal cartilages, with dorsal terminal 3 forming small spur.

This type of clasper structure is comparable with that of the *fullonica*-type of Stehmann (1969), the species of which have been included in the subgenus *Leucoraja* Malm, 1877. While the subgenus is represented by three species in the eastern North Atlantic, only one species is known from southern African waters, where it has been recorded at depths varying from 73 m to 445 m from west of Cape Point north to the Limpopo River mouth (Wallace 1967). Therefore, *Raja wallacei* like *R. fullonica*, shows a depth distribution into the upper limits of the archibenthal. Recently, Stehmann (1971*c*) has recognized a further species of the subgenus, *Raja* (*Leucoraja*) *leucosticta*, from the tropical waters of West Africa. This species had previously been confused with *Raja ackleyi*, Garman.

It has been pointed out that the cavity found on the outer surface of the dorsal lobe of the glans is formed in a different manner to the pseudosiphon and is related only to the musculature. However, the two cavities may prove to be related. As can be seen (Figs 34, 35) in both *Raja radiata* and *R. wallacei*, the dorsal terminal 3 cartilage is developed into a laterally projecting spur, which is large and S-shaped in *Raja radiata*, but smaller and less well developed in *Raja wallacei*. However, in the form and orientation of the accessory terminal 1 and 2 cartilages and in the ventral terminal, *Raja wallacei* shows a closer similarity to *Raja caudaspinosa*, *R. confundens*, *R. leopardus* and *R. dissimilis* (Figs 24, 26). Stehmann (1970) indicates an accessory terminal 3 cartilage in *Raja fullonica*, but not in *R. circularis* and *R. naevus*. Only two accessory terminals are found in *Raja wallacei*.

TYPE G: *Raja caudaspinosa* Von Bonde & Swart; *R. leopardus* Von Bonde & Swart; *R. confundens* Hulley; *R. dissimilis* Hulley; (and probably *R. ravidula* Hulley).

Claspers small and short, with or without dermal denticles on outer dorsal lobe; some specimens with a small cavity in musculature; two clefts or a cleft and a slit present; spike and sentinel small; rhipidion fan-shaped and usually associated with pent; shield not well developed; axial cartilage spatulate; four dorsal terminal cartilages; dorsal terminal 3 pointed, but not developed into lateral spur.

Species with this type of clasper structure have been grouped into the subgenus *Rajella* Stehmann (type-species *Raja fyllae*), which, in the North Atlantic, may also include the species *Raja garmani*, *R. erinacea*, *R. ocellata* and *R. lentiginosa*. On the basis of *Raja fyllae*, Stehmann (1970) confines the subgenus to the archibenthal, but depth distribution records for the South African species (Hulley 1970) indicate that some of the species may occupy the shelf areas (*Raja leopardus*), while others are known only from abyssal depths (*Raja dissimilis*, *R. ravidula*).

The presence of four dorsal terminal cartilages and the shape of the axial have already been discussed above in relation to Stehmann's ideas. Similarities in the accessory terminal 1 and 2, dorsal terminal 1 and ventral terminal cartilages, and the framework arrangement of dorsal terminals 2–4, can be seen between this group and Type F. However, the dorsal terminal 3 is differently developed.

TYPE H: *Cruriraja parcomaculata* (Von Bonde & Swart); *C. triangularis* Smith; *C. rugosa* Bigelow & Schroeder; (and probably includes *C. durbanensis* (Von Bonde & Swart)).

Claspers small and spatulate; dermal denticles usually absent, but one species with denticles on ventral border; thorn present on lateral edge of dorsal lobe, eperon on ventral lobe; inner dorsal lobe with pseudosiphon; rhipidion small and closely attached; knob and sentinel present; spike tongue-shaped and situated medially; axial cartilage characteristically J-shaped; dorsal terminal 1 enclosed by axial limb; terminal bridge between axial and accessory terminal 2.

This particular type of clasper structure is readily distinguished from all other types and is associated with the genus *Cruriraja*. In fact, it is further removed from the typical rajid type than *Bathyraja*, and, as in the case of the Anacanthobatidae, suggests that a further family within the Rajoidea be distinguished. Examination of the pelvic girdles and neurocrania seems to agree with this. A new family will therefore be defined (see page 78).

The genus is, at present, known only from two areas, the southern African coast (*Cruriraja durbanensis*, *C. parcomaculata* and *C. triangularis*), where the species inhabit shelf areas and the upper regions of the archibenthal, and the Gulf of Mexico (*Cruriraja atlantis*, *C. poeyi*, *C. rugosa* and *C. cadenati*), where they are recorded from archibenthal regions.

As has been pointed out, the predorsal caudal vertebral count (Vprd) is not species specific, but it would seem that in certain cases it may be used to distinguish between closely related species (Stehmann 1970; Hulley 1970) and may even be used for taxonomic discrimination at the subgeneric level. Stehmann (1970) suggests that *Raja alba* may be separated from the subgenus *Raja* by both Vtr and Vprd counts. While there appears to be some overlap in Vprd values for *Raja alba* and *R. clavata* in the eastern North Atlantic (Stehmann 1970: fig. 14), the counts for the southern African specimens appear to be well separated (Fig. 47), substantiating the recognition of *Rostroraja*, which was based on clasper structure.

The true significance of this method of application is open to question, since the separation of species on the basis of Vprd counts is not always supported by clasper distinctions. For example, in the southern African subgenus *Rajella*, two distinct species groups can be recognized (Fig. 47), but the clasper structure of the species *Raja leopardus*, *R. caudaspinosa*, *R. confundens* and *R. dissimilis* are almost identical. It is probable that with increasing knowledge, species of this particular subgenus, with intermediate values in Vprd count, may be found, as with *Bathyraja* and *Dipturus*.

Apparent differences seem to exist between *Bathyraja pallida* (Vprd 66–67) and *B. spinicauda* (Vprd 77–82) (Stehmann 1970). However, within this genus intermediate values have been recorded (Ishiyama 1958; Hulley 1970). Similarly, the high Vprd values for *Raja* (*Dipturus*) *nidarosiensis* (Stehmann 1970) are approximated by the southern African *Dipturus* species, *Raja pullopunctata* and *R. lanceorostrata* (Table 1), and are exceeded by the Japanese species *Raja macrocauda* and *R. gigas*.

While the shape of the anterior and posterior fontanelles may be species specific in bathyrajid species (Ishiyama 1958), marked differences are not evident in other rajids. It would appear therefore that neurocranial characters are mainly applicable above the species level. There can be no doubt that characters such as the structures of the rostral cartilage and appendices are of significant value in taxonomy (Bigelow & Schroeder 1948; Ishiyama 1952, 1958; Stehmann 1970). These have already been employed in the recognition of genera in southern African Rajidae (Hulley 1970). However, it appears that certain cranial characters can be used to separate the proposed subgenera of *Raja*, while the majority can best be interpreted in terms of the phylogenetic interrelationship between these subgenera.

Stehmann (1970) suggests that the length of the rostrum in relation to the cranial length may be used for the grouping of species and for the interpretation of phylogenetic relationships. He has pointed out that the rostral length is greater than the 'cranial length' (not cranial length of Hubbs & Ishiyama (1968: fig. 1) but equal to total cranial length minus rostral length) in *Dipturus*, but less than the 'cranial length' in all other subgenera of *Raja*. While high values for the rostral length/cranial length proportion are found in *Dipturus* species (Table 2), equally high values have been found for *Rostroraja*, and values above 50% have been found in *Raja confundens* and *R. ravidula*. Furthermore, the course of the hypothetical line drawn from the tip of the rostrum through the ophthalmic foramen appears to be a complex function of the rostral length and cranial width, and bears little relation to the suggested subgeneric groupings. However, *Dipturus* is characterized by the forward extension of the anterior fontanelle, so that in all species of this subgenus the rostrum is grooved, there being no definite anterior limit to the fontanelle. The extent of the rostral grooving varies in the different species (Fig. 50) and its presence can be regarded as primitive, since *Dipturus* shares this character with the Rhinobatidae.

The size of the nasal capsules varies to some extent. Enlarged capsules are found in *Raja robertsi*, *R. dissimilis*, *R. ravidula* and *R. spinacidermis* (Figs 52 D; 53 D; 54 D, E), a fact which seems to be correlated with depth distribution rather than proposed groupings, since these species (of different subgenera) are all found to occur at depths of 1 000 metres or more (Hulley 1970). Although no comparison was made of the number of Schneiderian and secondary folds or the number of sensory cells per unit area between these species and the continental shelf species, the massive development of the nasal capsules would substantiate the theory that olfaction is probably of greater importance in a deep-water habitat (Weichart 1951). As with the rostral length, the orientation of the nasal capsules bears little relationship to the groupings, but their shape, which is altered by the degree of development of the preorbital processes, may be of importance.

The preorbital process is well developed only in *Raja* and *Rostroraja* (Figs 51; 52 A), a character which these subgenera share with both the Rhinobatidae and with *Bathyraja* (Fig. 49 A; Ishiyama 1958: fig. 28; Stehmann 1970: fig. 27). This character, together with the orientation of the nasal capsules, may be employed to distinguish *Raja* and *Rostroraja* from the other subgenera. Similarly, the presence of a comparatively large postorbital process in *Bathyraja smithii* (Fig. 49 A) and other bathyrajids (Ishiyama 1958: fig. 28; Stehmann 1970: fig. 27) may be used as a taxonomic character for distinguishing this genus.

A marked degree of constriction of the neurocranium across the orbital region is characteristic of *Rajella* (Figs 53; 54 A, D), but the noticeable anterior displacement of the optic foramen and the position of the anterior cerebral vein foramen in this subgenus and in *Amblyraja* and *Dipturus* are best interpreted in terms of their phyletic relationship. The possession of a small orbito-nasal canal foramen in *Cruriraja parcomaculata* (Fig. 49 F) could be taxonomically employed, but further evidence is required from other species of this genus.

The jugal arches are angular and prominent in *Amblyraja* (Figs 52 D, E), in which they project as wing-like extensions from the laterally expanded auditory capsules. Angular arches are also found in *Rajella* (Figs 53; 54 A, D), but are directed postero-laterally from moderately expanded auditory capsules. In *Raja*, *Leucoraja* and *Rostroraja* (Figs 51; 52 A; 54 F), the jugal arches are more or less evenly curved and project posteriorly, while in *Dipturus* (Fig. 50) they are comparatively smaller and do not disrupt the contour of the auditory capsule region. In *Raja spinacidermis* (subgenus *Malacoraja*) (Fig. 54 E) the arches are poorly developed and thin, while in *Cruriraja* (Figs 49 D, E) they are particularly thin at their junction with the process of the hyomandibular facet.

The taxonomic significance of the shape and position of the posterior fontanelle is open to question, since these characters and even the differentiation into two posterior fontanelles vary within the same species (Stehmann 1970: figs 17, 19, 20, 24). As has been pointed out above, the shape of the anterior fontanelle is species specific in *Bathyraja*, and its shape and degree of development in other rajids are only suggestive of the subgeneric groupings, which are based on clasper structure.

In conclusion, it should be pointed out that while certain neurocranial characters, such as the constriction of the orbital region, the degree of development of the preorbital and postorbital processes, the orientation of the nasal capsules and jugal arches, and the shape and extension of the anterior fontanelle, may be used in combination as taxonomic characters at the subgeneric and generic level, their significance is more difficult to interpret than that of the clasper structure. However, they may be suitably employed in elucidating phyletic interrelationships.

To summarize, the southern African Rajidae can be identified within the framework of the genera and subgenera proposed by Stehmann (1970), which is based mainly on clasper structure, as follows:

Family **Rajidae**

Genus *Bathyraja* Ishiyama, 1968
  type-species *Raja isotrachys* Günther, 1877
  species: *Bathyraja smithii* (Müller & Henle, 1841)
Genus *Raja* Linnaeus, 1758
  type-species *Raja miraletus* Linnaeus, 1758
  1. subgenus *Raja* Linnaeus, 1758
    type-species *Raja miraletus* Linnaeus, 1758
    species: *Raja clavata* Linnaeus, 1758; *Raja straeleni* Poll, 1951
  2. subgenus *Dipturus* Rafinesque, 1810
    type-species *Raja batis* Linnaeus, 1758
    species: *Raja doutrei* Cadenat, 1960; *Raja pullopunctata* Smith, 1964; *Raja springeri* Wallace, 1967; *Raja lanceorostrata* Wallace, 1967; *Raja stenorhynchus* Wallace, 1967.
  3. subgenus **ROSTRORAJA** subgen. nov.
    type-species *Raja alba* Lacépède, 1803

Definition

Clasper massive, with pecten on outer dorsal surface, but without pseudosiphon; pseudorhipidion well developed; inner dorsal lobe with proximal cleft, but without distal slit or pocket; shield prominent with laminate integument; sentinel massive and situated far distally; spike and signal absent; four dorsal terminal cartilages, with pecten developed from outer lateral margin of dorsal terminal 3; ventral terminal with dorsally convex, wide, outer lateral margin. Rostrum produced and elongate, its length more than 50% of cranial length; nasal capsules moderately developed and orientated anteriorly; anterior cerebral vein foramen ventral.

  4. subgenus *Amblyraja* Malm, 1877
    type-species *Raja radiata* Donovan, 1808
    species: *Raja robertsi* Hulley, 1970
  5. subgenus *Leucoraja* Malm, 1877
    type-species *Raja fullonica* Linnaeus, 1758
    species: *Raja wallacei* Hulley, 1970
  6. subgenus *Rajella* Stehmann, 1970
    type-species *Raja fyllae* Lütken, 1888
    species: *Raja caudaspinosa* Von Bonde & Swart, 1923; *Raja leopardus* Von Bonde & Swart, 1923; *Raja confundens* Hulley, 1970; *Raja dissimilis* Hulley, 1970; *Raja ravidula* Hulley, 1970

Stehmann (1970) has defined a further subgenus, *Malacoraja*, based on *Raja mollis*. It is now considered that *Raja mollis* is synonymous with *Raja spinacidermis* Barnard (Hulley 1970). As no adult male specimen of this species has yet been taken, this identification is based on characters other than the clasper structure. Marked differences in the rostral length, the orientation and massive development of the nasal capsules and the poorly developed jugal arches, serve to distinguish *Malacoraja* from all other subgenera.

7. subgenus *Malacoraja* Stehmann, 1970
type-species *Raja spinacidermis* Barnard, 1923

The family Crurirajidae is now erected to include all species of the genus *Cruriraja*, which were formerly identified with the Rajidae.

Family **CRURIRAJIDAE** fam. nov.

Definition

Pectorals with radials of ordinary form, without lateral processes; outer margins of pelvics deeply notched, to form an anterior, limb-like structure, consisting of three articulated segments, externally distinct from the posterior, fin-like lobe of the pelvic; tips of anterior rays of pectorals falling short of tip of rostral cartilage; two dorsal fins. Otherwise external characters as for suborder.

Claspers small and spatulate; dermal denticles usually absent on dorsal border; thorn present on lateral edge of dorsal lobe, eperon on ventral lobe; inner dorsal lobe with pseudosiphon; rhipidion small and closely attached; knob and sentinel present; spike tongue-shaped and situated medially; axial cartilage characteristically J-shaped; dorsal terminal 1 enclosed by axial limb; terminal bridge between axial and accessory terminal 2.

Pelvic girdle simply transverse, with iliac regions moderately developed; one obturatorial foramen; prepelvic processes poorly developed; iliac processes large and recurved.

Neurocranium without preorbital and postorbital processes; orbito-nasal canal foramen small; jugal arches poorly developed; posterior cerebral vein foramen absent.

Genus *Cruriraja* Bigelow & Schroeder, 1948
type-species *Cruriraja atlantis* Bigelow & Schroeder, 1948
species: *Cruriraja parcomaculata* (Von Bonde & Swart, 1923); *Cruriraja durbanensis* (Von Bonde & Swart, 1923); *Cruriraja triangularis* Smith, 1964.

An interesting case is presented in the family Anacanthobatidae, which at present contains two genera, *Anacanthobatis* and *Springeria*. The discussion is only in relation to *Anacanthobatis marmoratus* and *A. americanus*, so that before definite taxonomic changes are made, *A. longirostris* from the Gulf of Mexico and *A. borneensis* from the South China Sea should be examined.

Basic major differences in clasper structure can be seen between *Anacanthobatis marmoratus* and *A. americanus* (Figs 10, 11, 43, 44), the most important of which is the absence in *A. americanus* of the ventral terminal cartilage. Hence there is a lack of an associated shield and eperon in the clasper glans in this species. Probably associated with this is the fact that the spike and sentinel in *Anacanthobatis americanus* are positioned laterally and are capable of rotation (Fig. 11). Furthermore, *Anacanthobatis marmoratus* lacks an external pseudosiphon, while in *A. americanus* there is an external pseudosiphon. Examination has shown that the structure and orientation of the cartilages is different in the two species.

It therefore appears that, on the basis of clasper structure, these two species should not be referred to the same genus and that the family Anacanthobatidae, as defined at present, may be diphyletic. In terms of priority, the South African species *Anacanthobatis marmoratus* becomes the type-species for the genus *Anacanthobatis*, which is then considered to be monotypic, while *Anacanthobatis americanus* should be referred to a new genus. Although Bigelow & Schroeder (1953) consider that a second South African species, *Anacanthobatis dubius* Von Bonde & Swart, 1923, can be referred to the genus *Springeria*, they later (1962) hold that *A. dubius* is probably an immature *A. marmoratus*, so that Wallace (1967) has synonymized the two under *Anacanthobatis marmoratus*. As the type specimens of these species are missing, this synonymy has been tentatively accepted.

Family **Anacanthobatidae**

Genus *Anacanthobatis* Von Bonde & Swart, 1923
    type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923
Genus *Springeria* Bigelow & Schroeder, 1951
    type-species *Springeria foliorostris* Bigelow & Schroeder, 1951
    species: *Springeria ori* Wallace, 1967

PHYLETIC INTERRELATIONSHIPS

White (1937) and Saint-Sienne (1949) consider that recent elasmobranchs, which do not include the archaic families Heterodontidae and Hexanchidae, arose from a common ancestor, which was not unlike *Palaeospinax* (family Heterodontidae). A monophyletic origin is also held by Disler (1966) on the basis of the embryonic development of *Trygon pastinacea*. Examination of the structure of the neurocranium led Holmgren (1941) to suggest a diphyletic origin for the recent Elasmobranchii, a view supported by Hasse's (1885) observations, and by Melouk (1947), who considers that the benthic mode of life is more primitive. However, it has now been shown that the features stressed by Holmgren (1941) represent minor ontogenetic modifications, and Schaeffer (1967) therefore considers separate origins for galeoids, squaloids and batoids, the latter probably arising from some benthic hybodont stock.

Within the batoid line, it is generally considered (Regan 1906; Leigh-Sharpe 1924; Holmgren 1941; Melouk 1947; Gregory 1951) that the Rajoidea arose from the Rhinobatidae, since they show a strong resemblance in dentition and in the possession of longitudinal folds on the tail. Ishiyama (1958), in comparing skull, rostral and clasper structure, arrives at the following conclusions:

(1) Rajids have arisen from a rhinobatid-like stock rather than a platyrhinid, since there is a trend in the reduction of basal segments in the myxopterygium and in denticulation, and a trend in the development of the clasper siphon.

(2) The genus *Bathyraja* originated directly from the ancestral stock, with subsequent neotonous modification of the rostral cartilage, but with retention of primitive characters in the clasper.

(3) Both *Raja* and *Rhinoraja* species can be derived from the bathyrajid-type, with the genus *Raja* representing an earlier split.

(4) Amongst the species of the genus *Raja*, those of the subgenus *Tengujei* (= *Dipturus*) are considered to be more primitive, since they show primitive characters in their rostral structure.

Stehmann (1970) has presented a phylogeny for the rajid species of the eastern North Atlantic, which, as has been shown above, form subgeneric groupings identical with those of the species of the southern African region. This phylogeny is based on clasper anatomy, rostral structure and geographic distribution. Stehmann (1970) selects the pseudosiphon as the definitive character, so leading to a division of the rajids into Rajidae I (without a pseudosiphon—*Dipturus*, *Raja*) and Rajidae II (with a pseudosiphon—*Bathyraja*, *Rhinoraja*, *Leucoraja*, *Amblyraja*, *Rajella*) (Fig. 55).

There is no doubt that the pseudosiphon is a primitive structure, and that

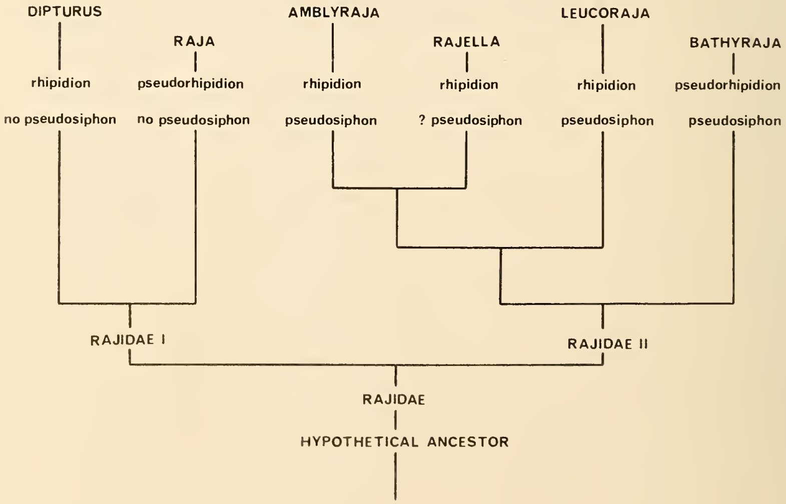

Fig. 55. Relationship within the Rajidae as suggested by Stehmann (1970), showing the possession of rhipidion, pseudorhipidion and pseudosiphon.

Ishiyama's (1958) interpretation of the ancestral nature of the genus *Bathyraja* is correct, for in this genus the ventral terminal cartilage is simple and not expanded into a lateral shield, the accessory terminal is reminiscent of *Rhinobatos*, and the axial cartilage is bluntly pointed rather than spatulate. Ishiyama (1958) also considers that the primitiveness of the group, especially the species *Rhinoraja kujiensis*, can be seen in the possession of scale on the ridge, and in the simple construction of the dorsal terminal 1 cartilage. However, it should be pointed out that the development of dermal denticles may be secondary, e.g. *Raja wallacei*, *R. leopardus*, *R. confundens*, and that the position of the dorsal terminal 1 in *Rhinoraja kujiensis* probably represents the case most removed from *Rhinobatos*, if we accept Ishiyama's theory of rotation of the dorsal terminal 1 from the ventral to the dorsal side of the clasper.

The genus *Bathyraja* represents a direct modification of the basic, ancestral stock, in which, by the process of neotony, the rostral bar is reduced to a thin rod. This may be related to an increased advantage in grubbing (Ishiyama 1958). The widespread, discontinuous, antitropical distribution of the genus (Hulley 1970) supports its antiquity, as does the possession of comparatively well-developed preorbital and postorbital processes in the neurocranium. *Rhinoraja*, with its segmented rostral bar, represents a further specialization of the bathyrajid condition, which would allow for even greater flexibility of the snout.

If the subgenus *Raja* is closely associated with the subgenus *Dipturus* (Stehmann 1970), then it must be accepted that the rhipidion was evolved twice (Fig. 55). However, the persistence of the pseudorhipidion, i.e. retention of a well-developed dorsal marginal cartilage, is evidence of an association of the subgenus *Raja* with the bathyrajid condition. This is supported by the simple form of the dorsal terminal 1 cartilage, with its proximal shelf for the insertion of the *m. dilatator*, conditions which approximate those found in Japanese bathyrajids (Ishiyama 1958: fig. 8). Furthermore, in the subgenus *Raja* the axial cartilage retains its primitive, terminal point. The proximal position and orientation of the dorsal terminal 2 can then be explained as a continuation of the trend in development of the dorsal terminal 2 and 3 cartilages from their position in *Rhinobatos* (Fig. 45) through some intermediate bathyrajid-like form (Ishiyama 1958: figs 10 K, D). The subgenus *Raja* may therefore be regarded as a side branch of the ancestral stock, close to the bathyrajid condition (Fig. 57), in which the pseudosiphon was lost (possibly with complete dorsal rotation of the dorsal terminal 1) and the ventral terminal more developed, but in which the neotonous condition of the snout was never retained. Rather there was a simple length reduction of the snout from its ancestral condition. In support of this, the neurocranium of *Raja* shows a closer affinity with that of *Bathyraja*, rather than with that of *Dipturus*. The preorbital process is well developed in *Raja* and *Bathyraja*, while its size and position in *Dipturus* approximates the condition in *Amblyraja*, *Rajella* and *Leucoraja*. Furthermore, the position of the foramen for the anterior cerebral vein in *Raja* approximates the bathyrajid condition, while in *Dipturus*, *Amblyraja*, *Rajella* and *Leucoraja*, it is displaced dorsally.

The acceptance of this proposition would mean that the rhipidion was only evolved once (Fig. 56), while the pseudosiphon, whose function is unknown, was lost in two separate evolutionary lines. This appears to be more acceptable than Stehmann's suggestion.

The subgenus *Rostroraja* appears to be associated with those groups in which the ancestral pseudorhipidion is retained. As has been pointed out above, it differs markedly from the subgenus *Raja* in axial shape, in the framework arrangement of the dorsal terminal cartilages and in the heavy development of the lateral edge of the ventral terminal cartilage. The possession of an elongate snout (the anterior fontanelle of which is not primitive) and a discontinuous distribution indicate a greater age for this group. This is supported by the Vprd count, which for *Raja alba* is quite distinct from that of the subgenus *Raja*. The higher count in *Rostroraja* (Fig. 47) is indicative of its greater age, so that this subgenus represents an early split from the *Bathyraja/Raja* line of evolution. The extreme ventral position of the anterior cerebral vein foramen would indicate a specialized condition, when compared with its median position in *Raja* and *Bathyraja*.

Some criticism may be levelled against this theory in terms of the accessory terminal cartilages, of which there are four in the subgenus *Raja*, two in *Rostroraja*, but only one in bathyrajids. However, a marked similarity can be seen between the extension of the ventral marginal cartilage of bathyrajid species and the tightly bonded accessory terminal 1 of *Rostroraja* and *Raja*.

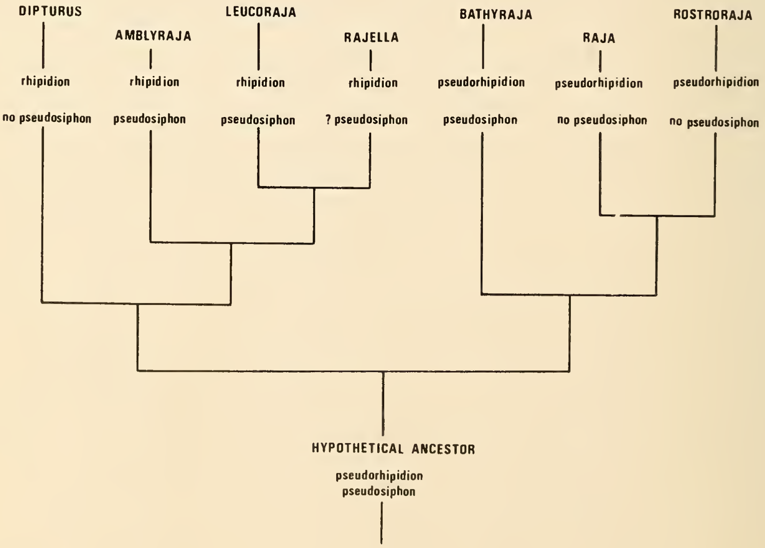

Fig. 56. Proposed relationship within the Rajidae, adapted from Fig. 57, showing the possession of rhipidion, pseudorhipidion and pseudosiphon.

Furthermore, the accessory terminals 3 and 4 might well be derived from laterally positioned dorsal terminal elements.

On the evidence presented by their distribution (Hulley 1966: fig. 8), both *Raja* and *Rostroraja*, which developed as shelf species from the boreal bathyrajid ancestors, penetrated the Mediterranean Subregion at the beginning of the Pleistocene glacial period (Klausewitz 1968). Possibly at this same time, a complete north–south distribution on the continental shelf may have been attained by *Rostroraja*, since equatorial cooling was pronounced along the eastern shores of the Atlantic (Hubbs 1952). The subsequent increase in sea temperatures at the end of the last glacial would have given rise to (?) equatorial submergence in the case of *Raja alba* (Hulley 1966), and would have induced a southerly spread of the subgenus *Raja*. This would then support Crowson's (1970) and Parin's (1970) ideas on the correlation between group age and distribution.

All other rajid subgenera in the eastern Atlantic can be derived from an ancestor, which possessed a pseudosiphon and long snout, and which had developed a shield and fleshy rhipidion (Fig. 57). In all, the longitudinally segmented pattern of the dorsal terminal cartilages, which form the framework of the dorsal lobe, is retained. This ancestor probably inhabited the archibenthal regions in boreal and antiboreal latitudes.

The subgenus *Dipturus* represents an early split from this ancestor, as indicated by the world-wide distribution of the group, in which the primitive, rigid, rostral bar, with elongate anterior fontanelle and grooved rostrum was retained, but in which the pseudosiphon was lost. The group apparently colonized the edge of the shelf and upper regions of the archibenthal, a fact which probably allowed for their subsequent spread to all oceans (Stehmann 1970). The low Vprd values in the southern African species of *Dipturus* seem to

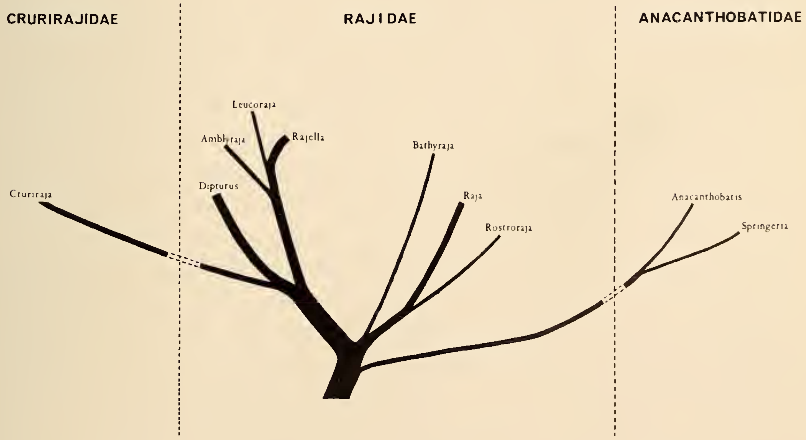

Fig. 57. Phyletic interrelationships as suggested by southern African Rajidae. The thickness of the lines corresponds to the relative number of species.

indicate that the group is not particularly ancient, but, as has been pointed out above, in several Japanese species of this subgenus, the count is somewhat higher (Ishiyama 1958). A strict interpretation of Vprd count to phylogeny would therefore mean that the origin of the subgenus *Dipturus* must be sought in areas other than the eastern North or eastern South Atlantic.

Examination of the clasper structure of *Breviraja colesi* (Ishiyama & Hubbs 1968) would seem to suggest that this genus can be closely associated with the *Dipturus* group. The species of this side branch penetrated the abyssal regions of the western central Atlantic, and, as in bathyrajids, retained the neotonous condition of the snout as an increased advantage in grubbing.

Although Stehmann (1970) suggests an association of *Amblyraja*, *Leucoraja* and *Rajella* with the bathyrajid condition, Rajidae II (Fig. 55), a closer affinity with the subgenus *Dipturus* is now evident. Not only are there similarities in the structural arrangement of the cartilages and in the presence of a well-developed rhipidion and strongly developed shield, but there are also marked resemblances in the dorsal terminal 1, ventral terminal and accessory terminal 1 cartilages. Similarly these subgenera share common neurocranial characters with *Dipturus*. They do not have well-developed praeorbital processes and the position of the anterior cerebral vein foramen is always dorsal to the optic foramen.

In terms of the pseudosiphon, it would appear that *Amblyraja* might be considered to be ancestral to both *Leucoraja* and *Rajella*, and Stehmann (1970) goes as far as to derive *Rajella* directly from *Amblyraja*. Counts of the number of predorsal caudal vertebrae show a low value for *Amblyraja* (48–52) and a high value for *Rajella* (55–73), suggesting that *Rajella* might be the more primitive. However, the subgenus *Amblyraja* has a much wider distribution in the Atlantic than either of the other two subgenera, and, in terms of the evolution of the clasper, particularly the retention of the pseudosiphon, may be considered to be an early split from the *Leucoraja/Rajella* line.

The phylogenetic position of *Raja spinacidermis*, as based on Vprd count, is not clear, although comparatively high values indicate an age equivalent to that of the subgenus *Amblyraja*, with the possibility of an even greater age. It must be emphasized that the validity of *Malacoraja* as a separate subgenus rests solely on its peculiar spination pattern, rostral length, nasal capsule orientation and depth distribution, the taxonomic values of which are uncertain. But until examination of the clasper structure can be made, Stehmann's (1970) proposals must be accepted.

The claspers of the genus *Cruriraja*, which possess a shield and pitted rhipidion, but lack an external pseudosiphon, bear a marked resemblance to those proposed for the ancestral *Dipturus* stock. However, there are major differences, especially in the arrangement of the dorsal terminals. The comparatively high values of the Vprd count in both *Cruriraja parcomaculata* and *C. triangularis* would seem to indicate an early split from the ancestral to the crurirajid condition (Fig. 57). The structure of the clasper of the mid-western Atlantic species *Cruriraja rugosa* appears to be much simpler than that of the southern African species, particularly as regards the accessory terminals. While noting that a simpler structure may not necessarily mean more ancestral (Mayr 1969), the structure of the shield in *Cruriraja rugosa* approximates more closely to the ancestral condition. Furthermore, the Vprd count for *Cruriraja rugosa*, which is based on a single specimen only, is slightly higher than that of the southern African species. However, before theories are advanced as to the possible method of evolution, i.e. west to east migration (cf. Clinidae: Springer 1970), the archibenthal and abyssal rajid fauna of the tropical western Atlantic needs further examination.

The evolutionary position of the Anacanthobatidae is not evident at this stage, for, as has been pointed out, on the basis of the clasper structure of *Anacanthobatis marmoratus* and *A. americanus*, the group as defined as present appears to be diphyletic. *Anacanthobatis americanus*, which is now considered to belong to another genus, appears to be closer to the *Dipturus* ancestral stock and its lack of a shield can be seen as the ultimate case in the general trend in reduction of that structure, which is shown by *Amblyraja*, *Leucoraja* and *Rajella* species. The possession of similarly formed pelvic girdles but structurally different clasper arrangements can therefore only be interpreted as an early origin for the family (Fig. 57). This theory is tentatively advanced until examination of further anacanthobatid material becomes possible.

In conclusion, it must be emphasized that, unlike the majority of South African marine fishes, which appear to have their origin in the central Indo-Pacific (Smith 1961), the Rajidae show a closer affinity with the eastern North Atlantic. This is not surprising, since the tropical East African region apparently forms a barrier zone, in which rajids have never been recorded (Playfair & Günther 1866; Peters 1868; Fourmanoir 1954; Smith & Smith 1963).

A warm-water barrier zone to temperate species has apparently been in existence in this region since early Permian times, when a palaeo-equatorial current impinged on the African–Arabian coastline (Frakes & Crowell 1970). This is well before the proposed mid-Cretaceous origin of the Rajidae (White 1937). During the Pleistocene period, when major colonization of the southern African shelf region was in progress (M. M. Smith 1970), this tropical barrier was probably not broken down, as it was in the tropical eastern Atlantic (Hubbs 1952). The following hypothesis is offered in support.

Biggs (1966), on the basis of endemism in fishes of oceanic islands, has shown that Pleistocene temperature fluctuations have not been the same in all oceans. Similar conclusions have been reached by Ericson *et al.* (1964) and Emiliani (1970) on palaeontological evidence.

During the periods of glaciation, the Northern Hemisphere was characterized by a southern spread of the polar ice. This had a marked effect in lowering sea temperatures, especially where the thermal capacity of the ocean was small and where the ice was in direct contact with the sea, e.g. North Atlantic. This resulted in a southerly displacement of certain species. However, in the Southern Hemisphere, glaciation was comparatively slight (Charlesworth 1957). Coupled to this is the fact that the Indian Ocean is bounded to the north by a continental mass, rather than an ice-cap, so that while extensive glaciation may have occurred in the Himalayan region, this only had a localized effect on the sea temperatures.

Therefore, because of the lack of a northern boundary ice-cap and because the major portion of the Indian Ocean is situated south of the equator, it is held that the tropical marine environment of the East African region did not vary during the Pleistocene. This is supported by Cox (1927: 18), who states for Mollusca that 'there is no evidence for the invasion of the area by colder water forms in Pleistocene times'. The East African region has therefore always formed an effective barrier zone to the migration of the Rajidae.

The southern African region has therefore been one of secondary colonization rather than primary development, and the Rajidae can be envisaged as arising from two sources:

(1) an older Gondwanaland distribution: these ancestral forms, i.e. *Bathyraja*, *Dipturus*, probably had their origin in some other region. In the Southern Hemisphere at least they were distributed in the area of the Cape sulcus (Frakes & Crowell 1970), which was in existence until the end of the Jurassic. This would mean that these forms arose from the rhinobatid stock somewhat earlier than the proposed mid-Cretaceous origin for '*Raja*' proposed by White (1937);

(2) a later north to south distribution, following the continental shelf and slope regions: these subgenera (*Raja*, *Amblyraja*, *Leucoraja*, *Rajella*) probably had their origin in the North Atlantic, and penetrated the southern African region in a series of waves, the most recent dating from the end of the last glacial period of the Pleistocene.

Distribution

Skates are widely distributed in all oceans, where they occur from polar (Clark 1926; Nikolskii 1961; Andriashev 1966) to tropical latitudes (Fowler 1936; Bigelow & Schroeder 1962; Blache *et al.* 1970; Hulley 1972), but have their greatest species diversity in warm temperate and boreal latitudes (Bigelow & Schroeder 1953; Stehmann 1970). However, they have never been recorded from Micronesia, Polynesia, Hawaii and the tropical region of East Africa, around Zanzibar. Although found predominantly on the continental shelf and upper regions of the slope, recent investigations have shown that skates are present in archibenthal and abyssal regions (Garrick 1965; Forster 1965; Hulley 1970). Besides brief descriptions given by Barnard (1925), Norman (1935), Smith (1961) and Wallace (1967), no detailed account of the distribution of southern African Rajidae has been given, although Hulley (1966, 1969) has commented on the distribution of *Raja pullopunctata*, *R. clavata*, *R. alba* and *R. miraletus*.

The limits of the southern African region have been variously defined (Barnard 1925; Knox 1960; Smith 1961; Day 1967; Penrith 1970) and appear to depend largely on personal choice. For the purposes of this discussion, the southern African region, as defined by Barnard (1925) has been used; that is, the subcontinent south of the fifteenth parallel, extending from about Moçâmedes in southern Angola on the west coast, to north of the Zambezi River mouth in Moçambique on the east, and taken down to a depth of 1 000 metres. The northern limits of this region on the west coast have been fairly well covered by research cruises of the *Mercator*, *Walther Herwig*, *Atlantide* and the Belgian South Atlantic Expedition, while the area north of Beira on the east coast has been covered during Cruise 8 of R.V. *Anton Bruun*.

The distribution of the dominant elements of the intertidal flora and fauna of South Africa has been summarized by Stephenson (1939, 1944, 1948), who, on the basis of surveys of rocky intertidal shores, recognized three faunal provinces with areas of overlap between them: the west coast, from the Orange River mouth to Cape Point; the south coast, from Cape Agulhas to Port Elizabeth; and the east coast, from Port St. Johns to northern Natal. In discussing the distribution of polychaete worms, Day (1967) considers that the west and south coasts are not distinct below the intertidal zone, and has pointed out that bottom temperatures at 100 metres (12°–14°C) are uniform from Port Elizabeth to Lüderitzbucht. He recognizes four faunistic provinces in southern Africa:

(1) the Moçambique–Madagascar province, dominated by tropical species: this reaches Lourenço Marques;

(2) the Natal province, with tropical species, but also with fair numbers of endemics and Atlantic species; this reaches Bashee River;

(3) the Cape and South West African province, dominated by endemics, but with a few tropical and several other components;

(4) the Angola province, dominated by tropical West African species: this extends north of Cape Frio. Penrith & Kensley (1970*a*, *b*) suggest that the southern limit of this province may extend to between Lüderitzbucht and Walvis Bay, at least intertidally.

These faunal provinces allow for the greatest number of generalizations and, since certain of the boundaries remain speculative, may be expanded or contracted to suit the discussion of particular groups of organisms. Fishes, however, are unsuitable subjects on which to base conclusions regarding faunal distribution boundaries, owing to their mobility. In his discussion on the zoogeography of the fishes of the Indian Ocean, Cohen (1971) postulates that the 20°C isotherm is the most reliable parameter marking the boundary between tropical and temperate waters, and limits the tropical region of the east coast to Natal. Myers (1939) considers that the boundary of the tropical Indo-Pacific is best defined by the distribution of the genus *Scarus* (Pisces, Callyodontidae), which would mean that, as far as the ichthyofauna is concerned, the boundary of the tropical region may be further south, in the region of East London. Smith (1961) places the boundary of the Indo-West Pacific at Great Kei River mouth.

On the basis of distribution beyond the limits of the southern African region, the ichthyofauna has been divided into seven categories (Barnard 1925; M. M. Smith 1970): deep and mid-water species; cosmopolitan and circumtropical species; Indo-Pacific species; Atlantic species, confined to the west coast; austral species; eastern Atlantic and Mediterranean species, which pass around Cape Point to various points on the east coast; and endemics. The distribution of these categories is intimately connected with hydrographic conditions (M. M. Smith 1970).

The known latitudinal and depth distributions of the 22 species of Rajidae, recorded from the southern African region, are shown in Figures 58, 59, while the frequency of occurrence is given in Table 3. The sampling data does not allow for comment on the relative abundance at various depths and hence the variation in depth distribution with latitude.

Of the species, 13 are endemic, 8 are known from the eastern Atlantic, and 1 species is also reported from Kerguelen. Of the endemics, *Cruriraja durbanensis*, *Raja dissimilis*, *R. ravidula* and *R. robertsi* are known only from the west coast; *Raja leopardus* and *R. caudaspinosa* are probably confined to the west coast, but have been recorded once from the east coast; *Cruriraja triangularis*, *Raja stenorhynchus*, *R. springeri* and *R. lanceorostrata* are known only from the east coast; while *Cruriraja parcomaculata*, *Raja pullopunctata* and *R. wallacei* have been recorded both east and west of Cape Point. It is remarkable that no Indo-Pacific species of Rajidae are known from the southern African region, and a theory has been advanced to explain this phenomenon (see page 85).

Bottom temperatures, corrected to the nearest degree, at various depths throughout the southern African region have been taken from Rand (1965), Bang & Pearse (1970), Annual Reports of the Division of Sea Fisheries (1958, 1960, 1961, 1962, 1964) and unpublished station lists of R.V. *Meiring Naude*, and are summarized in Table 4. For latitudes 17°S to 34°S on the west coast, the range in bottom temperatures over a three-year period is given, while at other positions, temperatures from a single cruise tract are shown. It should be noted that the temperatures have mainly been taken from reversing bottles, so that the temperature at sounding depth is not available; the discrepancy varies from 5 metres inshore to 100 metres in depths over 300 metres. However, the records are only used to show major trends in temperature variation.

TABLE 3

Frequency of occurrence of southern African Rajidae. Rare/little known = 2–6 records; regularly present = 6–50 records; common = more than 50 records.

Single record only	Rare/little known	Regularly present	Common
C. durbanensis	*R. springeri*	*R. pullopunctata*	*R. alba*
R. stenorhynchus	*R. spinacidermis*	*R. confundens*	*R. miraletus*
R. lanceorostrata	*R. ravidula*	*C. parcomaculata*	*R. clavata*
R. dissimilis	*R. doutrei*	*C. triangularis*	*R. straeleni*
R. robertsi	*R. radiata*		*R. caudaspinosa*
	B. smithii		*R. leopardus*
			R. wallacei

TABLE 4

Bottom temperatures, corrected to the nearest degree, in the southern African region.

WEST COAST

Latitude	Depth (metres)	Temperature (°C)
9°S	30	23°
	60	20°
	100	15°
	300	12°
	1 000	4°
17°S	50–99	13–15°
	100–149	13°
	150–199	—
	200–299	12°
	300–800	5–12°
	1 000	3–4°
19°S	50–99	12–14°
	100–149	13–14°
	150–199	13–14°
	200–299	12–13°
	300–800	5–6°
	1 000	4°
21°S	50–99	12–14°
	100–149	12–13°
	150–199	—
	200–299	11–12°
	300–800	4–11°
	1 000	4°
23°S	50–99	11–13°
	100–149	10–13°
	150–199	—
	200–299	10–11°
	300–800	5–10°
	1 000	3°
25°S	50–99	10–12°
	100–149	10–12°
	150–199	12°
	200–299	10–11°
	300–800	8–11°
	1 000	3–4°
26,5°S	50–99	11°
	100–149	9–11°
	150–199	10–11°
	200–299	9°
	300–800	4–10°
	1 000	3–4°
29°S	50–99	9–11°
	100–149	9–11°
	150–199	9–11°
	200–299	—
	300–800	10°
	1 000	3°
30,5°S	50–99	—
	100–149	9–10°
	150–199	8–10°
	200–299	8–9°
	300–800	4–6°
	1 000	3°
32°S	50–99	9–10°
	100–149	8–9°
	150–199	9°
	200–299	—
	300–800	7–9°
	1 000	3°

WEST COAST (*continued*)

Latitude	Depth (metres)	Temperature (°C)
34°S	50–99	9–10°
	100–149	10°
	150–199	—
	200–299	8–10°
	300–800	5–8°
	1 000	3°

AGULHAS BANK

Latitude	Depth (metres)	Temperature (°C)
S	30	16°
Mossel Bay	80	10°
	350	7°
	1 000	5°
S	50	10°
Knysna	100	10°
	900	4°
	1 000	4°
S	100	11–12°
Plettenberg Bay	200	12°
	400	7°
	1 000	4°
S	70	12°
Port Elizabeth	200	8°
	800	5°
	1 000	5°
S	50	12°
East London	400	11°
	600	11°
	1 000	5°

EAST COAST

Latitude	Depth (metres)	Temperature (°C)
33°S	70	15°
	1 000	5–7°
32°S	600	8°
	1 000	5–6°
31°S	50	21°
	800	8°
	1 000	6°
29°S	150	16°
	1 000	5°
28°S	300	12°
	400	9–12°
27°S	400	11°
	600	9°
	800	9°
	1 000	4°
26°S	30	24°
	400	10°
	600	9°
	2 000	2°

Discussion

Classic zoogeography, which is concerned with the distribution of taxa in relation to physical and chemical parameters, rests solely on two foundations: the correct identification of the particular taxon on a world-wide basis, and extensive sampling, especially towards the limits of ranges, where specimens dwindle in numbers. Unfortunately, as far as rajids are concerned, both criteria have not been fully met. The new approach to rajid systematics is still in its infancy, and only the faunas of the western North Pacific (Ishiyama 1967), eastern North Atlantic (Stehmann 1970) and eastern South Atlantic (Hulley 1970) have been extensively examined. Furthermore, in the southern African region the majority of specimens have been taken by commercial trawlers, fishing between 250 and 900 metres, so that for the west coast at least there are few inshore records.

In certain instances, confusion of specimens and their localities rather than misidentification has taken place. This is obviously the case with Von Bonde & Swart's paper (1923), in which the type locality for *Cruriraja durbanensis* is given as 30°10.00'S, 14°38.00'E in 859 metres, i.e. west coast, whereas the specific name indicates east coast, while the type localities for *Raja leopardus* and *R. caudaspinosa* are given as off Natal in 512 metres. Since the paratype of *Raja albalinea* (= *Raja caudaspinosa*) was also taken at 512 metres, but at 32°3.00'S, 16°2.00'E, and since these two species have not been recorded from Natal by Wallace (1967), it is considered that they are confined to the west coast.

While other factors such as salinity and bottom topography may play an important role in determining the distribution patterns of fishes (Gilchrist 1905; M. M. Smith 1970; Zoutendyk, personal communication), temperature has been considered the most determinate parameter (Ekman 1953; Hedgepeth 1957; Cohen 1971), and it is within this context that the distribution of southern African Rajidae will be considered. The effect of temperature can be twofold (Penrith 1970): it can act directly on the species concerned, or act in an indirect manner in limiting other organisms, which make a particular habitat more suitable. The ecology of the southern African Rajidae is still too little known to estimate the relative importance of direct and indirect influence of temperature.

Although no fish family is endemic to the southern African region, the degree of endemism at the species level in this region appears to be somewhat higher than in the Mediterranean or Galapagos Islands (Tortonese 1963; Rosenblatt & Walker 1963), and has been estimated at 31,5% (Barnard 1925). A lower value of 25,4% has been estimated by M. M. Smith (1970: 5), but she considers that 'true endemics' cannot be considered to come from deeper than 200 metres, as 'it is merely a matter of time and opportunity before they are found in other parts of the oceans'. There is no doubt, at least among elasmobranchs (Hulley 1971) that this is true, where the number of endemics is being constantly reduced with further systematic work. However, the estimated values approximate to that given by Day (1967) for polychaetes (36%). The percentage endemism varies from family to family; in some the value may be as high as

70% (Scyliorhinidae: Barnard 1925) and 100% (Clinidae: Penrith 1970). Stehmann (1970) indicates that of 22 species of Rajidae represented in the eastern North Atlantic 11 (50%) are endemic, and it would seem, therefore, that the value of 59,1% for the southern African rajid fauna is reasonable. There are no endemic genera or subgenera in the southern African region. All are represented in the eastern North Atlantic. Not only this, but the specific composition of the southern African rajid fauna shows a closer affinity with this region (Hulley 1970).

Day (1967) and Penrith (1970) have pointed out that the Cape/South West African province is dominated by endemics, and this is true of rajids, where 46,2% are confined to the west coast, while only 32,2% are entirely east coast in distribution. However, *Cruriraja durbanensis*, *Raja stenorhynchus*, *R. lanceorostrata*, *R. dissimilis* and *R. robertsi* are only known from their type localities. I consider their distribution too imperfectly known to be discussed further here.

Only one species, *Raja miraletus* (Fig. 59), shows discontinuous distribution in the southern African region, as defined. This species has been recorded from the Mediterranean (Clark 1926) and extends southwards along the north-west African and West African coasts, being recorded from Morocco (Clark 1926), Cape Bojador (Murray & Hjort 1912), Rio de Oro, Cape Blanc to Cape Verde (Pellegrin 1914), Senegal (Cadenat 1950) and from Cape Lopez in Gabon to Baie les Tigres in Angola (Fowler 1936; Poll 1951; Krefft 1968*a*). The southernmost record for the species at 18°30′S, 11°27′E was taken by FFS *Walther Herwig* (Hulley 1970). It is absent from regions further south, but is recorded in False Bay and extends northwards along the east coast to Richard's Bay (Wallace 1967).

While depth distribution records (Fig. 58) indicate that the species may occur down to 440 metres, Poll (1951) points out that *Raja miraletus* is essentially a shallow-water species, most abundant between 50 and 150 metres, where temperatures vary between 24,1°C and 12,7°C. From Table 4 it can be seen that for depths up to 200 metres on the west coast, a bottom temperature of 13°C or above is maintained as far south as about 19°S, but that from about 21°S to 34°S, the minimum temperature at 200 metres is lower, although at shallower depths may be between 12°C and 14°C as far south as about 23°S. This would suggest that this dominant member of the tropical West African fauna has a lower limiting temperature of about 13°C, and that its most southerly record (18°30′S) might mark the boundary zone from tropical West African to cold west coast fauna.

From False Bay to Durban, *Raja miraletus* is commonly taken in depths less than 100 metres, where temperatures vary seasonally (Bang, personal communication) between 9°C and 14°C. Although the present data allows for no prediction of onshore and offshore seasonal migrations of this species over the Agulhas Bank, it appears that the limiting temperature for *Raja miraletus* in this region may be slightly lower than on the west coast, i.e. there may be physiological differences between West African and South African specimens. It

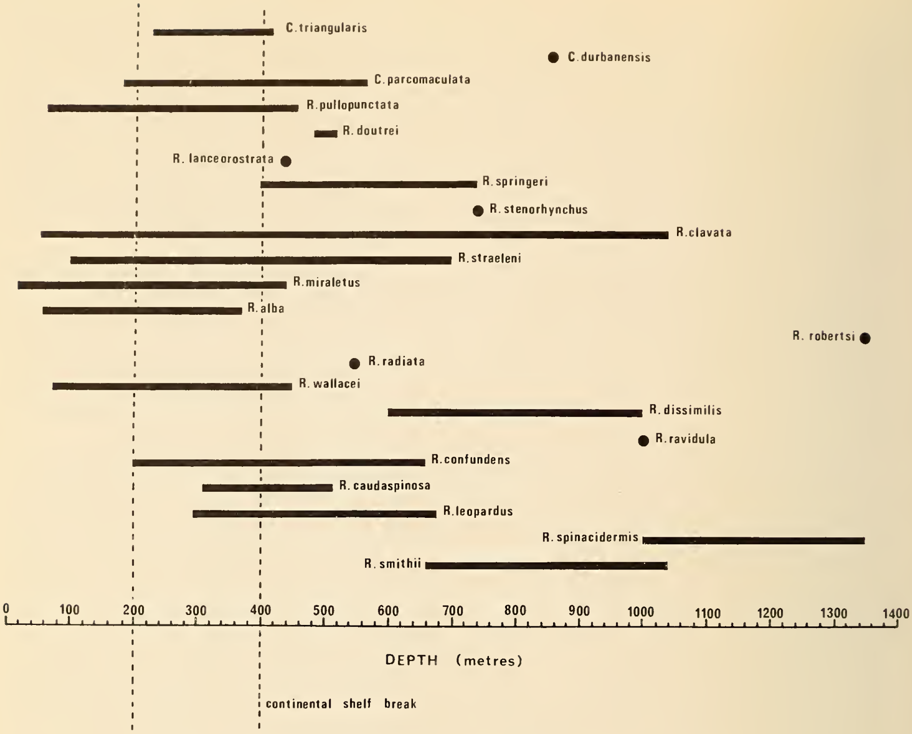

Fig. 58. Depth distribution ranges of southern African Rajidae.

should be pointed out that there are some morphological details (Hulley 1969) which would substantiate the distinction of a South African subspecies. Although the most northerly record on the east coast is at Richard's Bay, bottom temperatures indicate that the species could inhabit waters further to the north (Table 4).

Two other species found in tropical West African waters also penetrate the southern African region. *Raja straeleni* is common between 20°N and 15°S (Blache *et al.* 1970). Poll (1951) points out that this species, which inhabits colder waters than *Raja miraletus*, has regularly been taken in depths greater than 200 metres in this region, but may be found in shallower depths in more southerly latitudes. Temperatures at 200 metres in the tropical region vary from 11,6°C to 15,75°C (Poll 1951). From Table 4 it would appear that for depths greater than 200 metres, a lower limiting temperature of about 12°C occurs in the region between 21°S and 23°S. The most southerly record of this species at 22°03′S, 13°12′E (Fig. 59) would substantiate this temperature limit. Again it can be seen that inshore temperatures remain higher from 23°S to about 29°S, which would mean that the species may be expected to be found at shallower depths in this region.

Raja doutrei, the other tropical West African species, has been taken off the coast of Senegal (Cadenat 1960) at a depth of 450–600 metres, where bottom temperatures are in the order of 6°–10°C (Ingham 1970). This would mean that *Raja doutrei* would be capable of extending as far south as Cape Point, although its most southerly record to date is only 27°S.

Therefore, on the basis of rajid distribution alone, the southern boundary of the tropical West African fauna cannot be accurately fixed, since the temperature dependency of each species varies considerably. However, the distribution pattern of the only inshore species, *Raja miraletus*, would support the recognition of a boundary zone between 18°S and 20°S, as proposed by Penrith & Kensley (1970*a*, *b*) for rocky intertidal shores.

The phenomenon of bipolar (antitropical) distribution is well reported in the Rajidae (Hubbs 1952; Bigelow & Schroeder 1953; Hulley 1966; Krefft 1968*b*; Stehmann 1970), where certain species exhibit equatorial discontinuity in latitudinal distribution. Four species in the southern African region show this type of distribution pattern, which in this instance should be termed antitropical rather than true bipolarity. *Raja clavata* and *R. alba* are known from the eastern North Atlantic and Mediterranean (Clark 1926; Stehmann 1970), and extend southwards to about 20°N (Cape Blanc). They are not recorded over the tropical West African region, but reappear in the waters off South West Africa, from where they extend around Cape Point to Barra Falsa in Moçambique (Wallace 1967), southern Madagascar and Mauritius (Hulley 1966: fig. 8). In order to allow for gene flow from north to south and vice versa, equatorial submergence of these species probably takes place, so that it is possible that they will be discovered in deeper waters in tropical latitudes along the West African coast. The records of both species east and west of Cape Point (Fig. 59) support the idea of suitable, uniform temperatures for the west, south and east coasts at depths greater than 100 metres. It should be noted that the temperature range at 100 metres, 12°–14°C, given by Day (1967) appears to be somewhat high, for although there are seasonal variations, the temperatures east and west of Cape Point at 100 metres vary from 9°C to 10°C (Table 4).

It is interesting to note (Fig. 59) that, in the South Atlantic, *Raja clavata* appears to have a northern limit at about 23°S, and is replaced by the closely allied species, *R. straeleni*, over the area 22°S to 15°S, in the southern African region. Direct temperature dependence seems an insufficient explanation for this, and it is probable that competition between the species plays an important role in limiting the spread of *Raja clavata* towards the end of its possible temperature range at that depth, since both species have a similar depth distribution range (Fig. 58).

The other species exhibiting antitropical distribution patterns, *Raja spinacidermis* and *R. radiata*, also show an east/west distribution in the North Atlantic (Stehmann 1970). In the southern African region, *Raja radiata* is known from a single record (Fig. 59) and *Raja spinacidermis* only from deep water off Cape Point (Hulley 1970), so that it is impossible to comment further on their distribution.

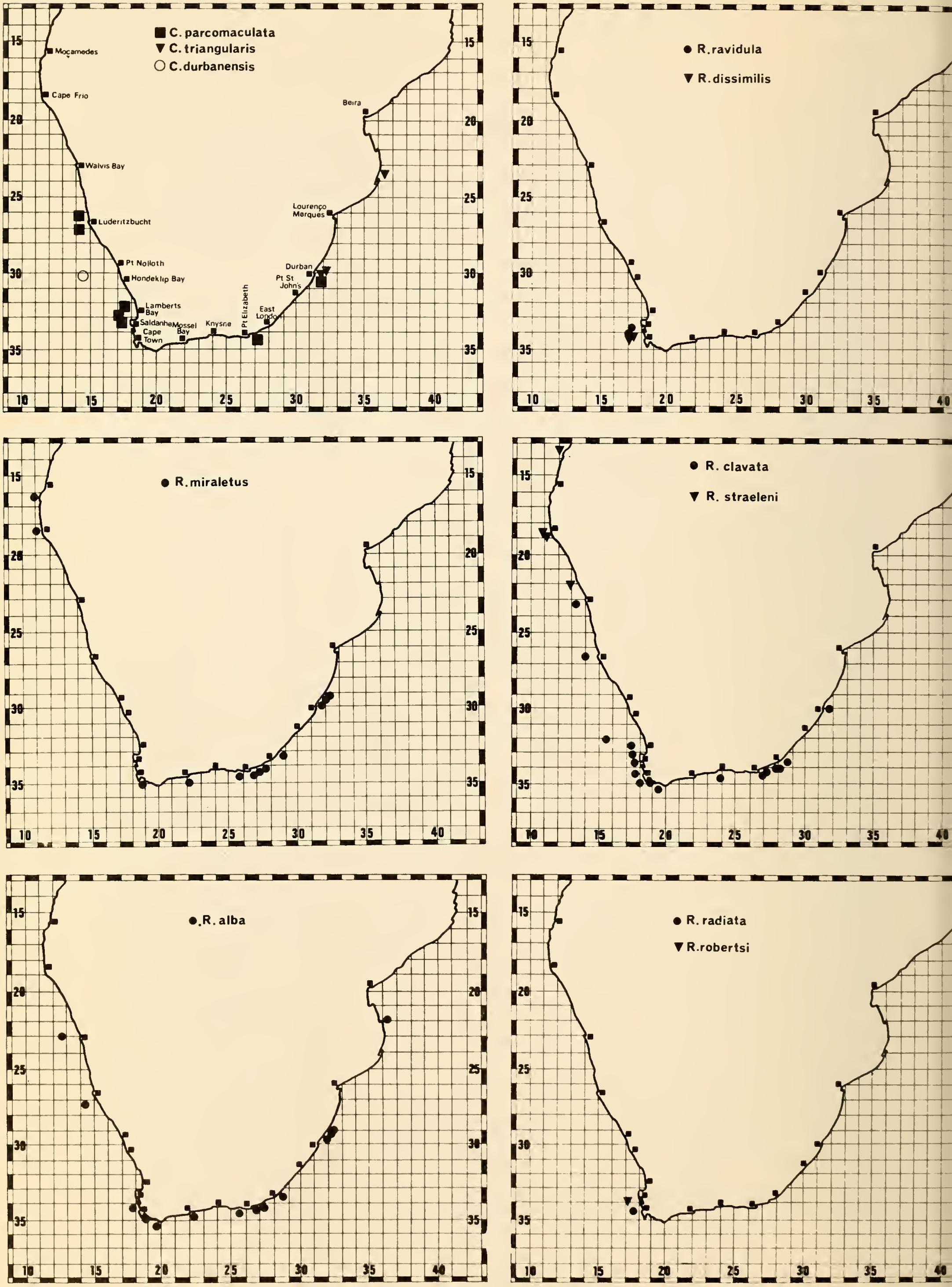

Fig. 59. Distribution of Rajidae and Crurirajidae in the southern African region. Open symbols indicate doubtful records.

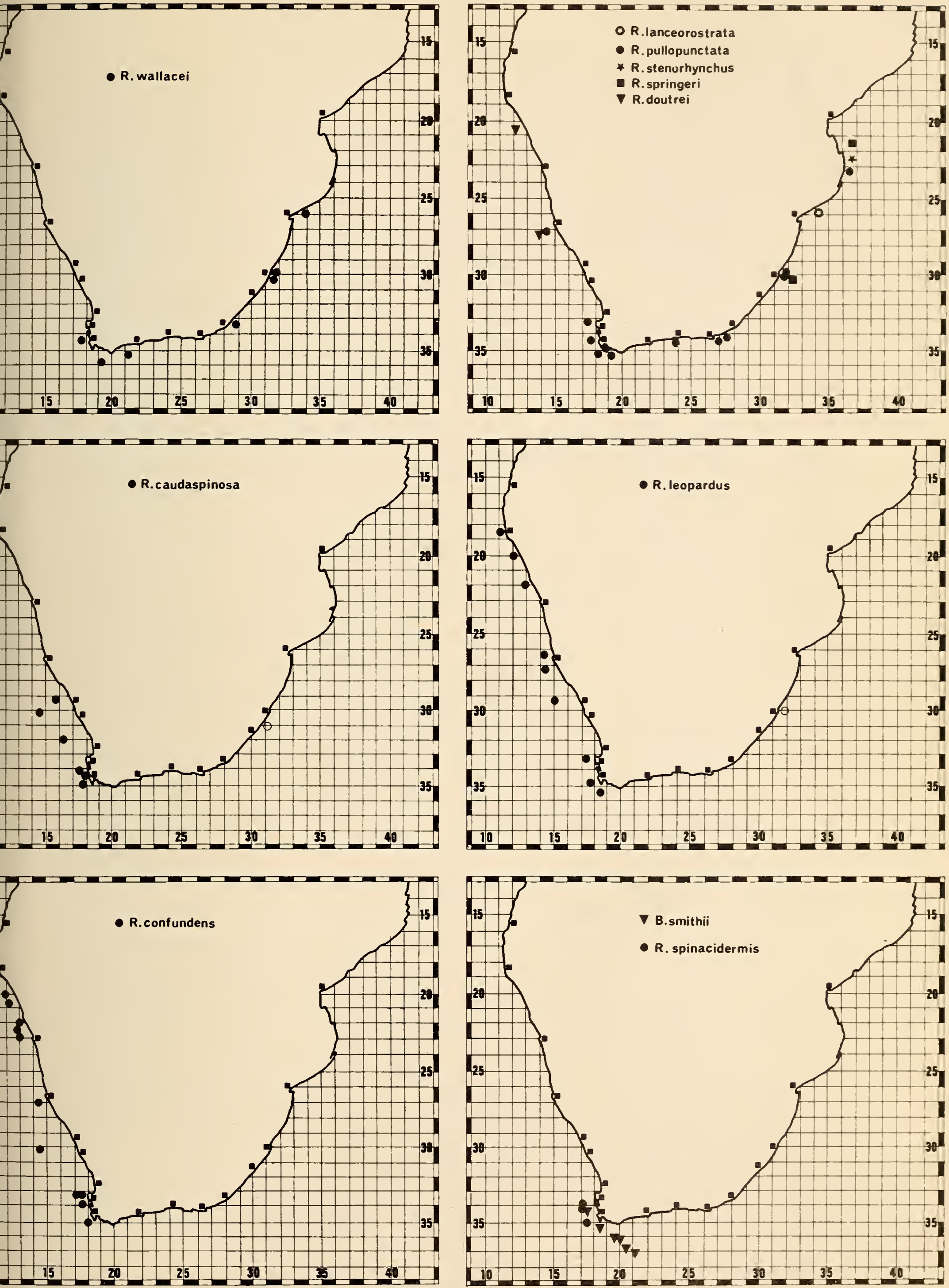

Fig. 59. (*continued*)

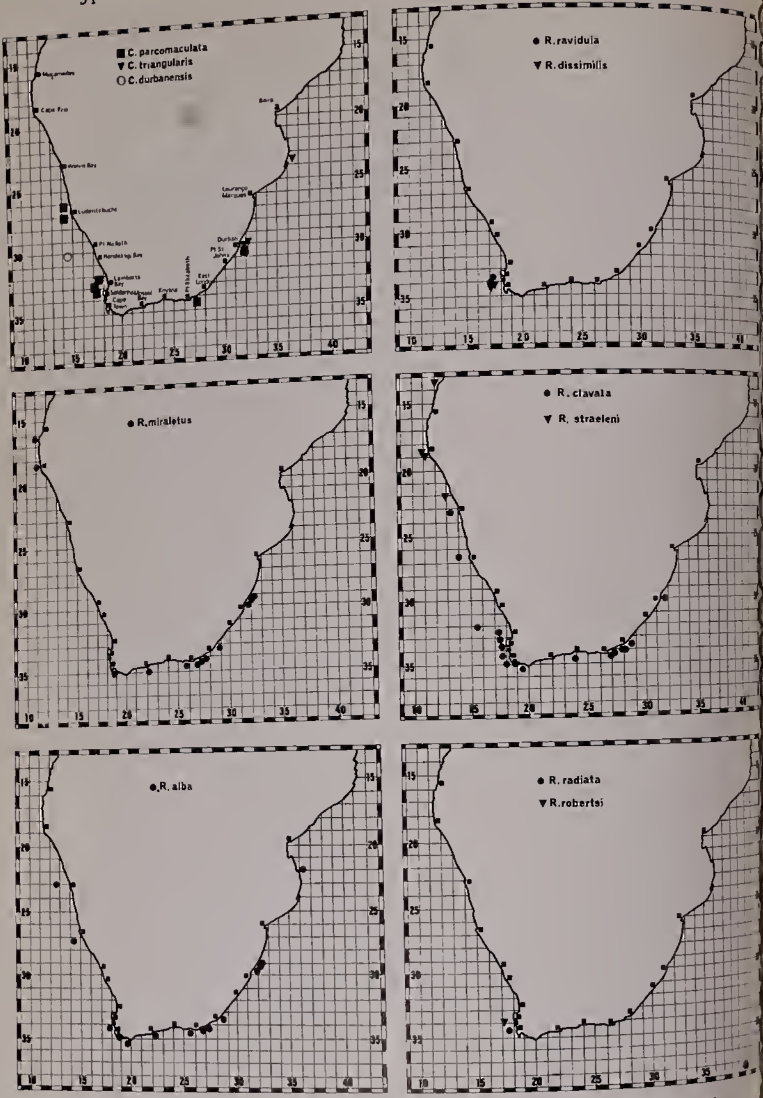

Fig. 59. Distribution of Rajidae and Crurirajidae in the southern African region. Open symbols indicate doubtful records.

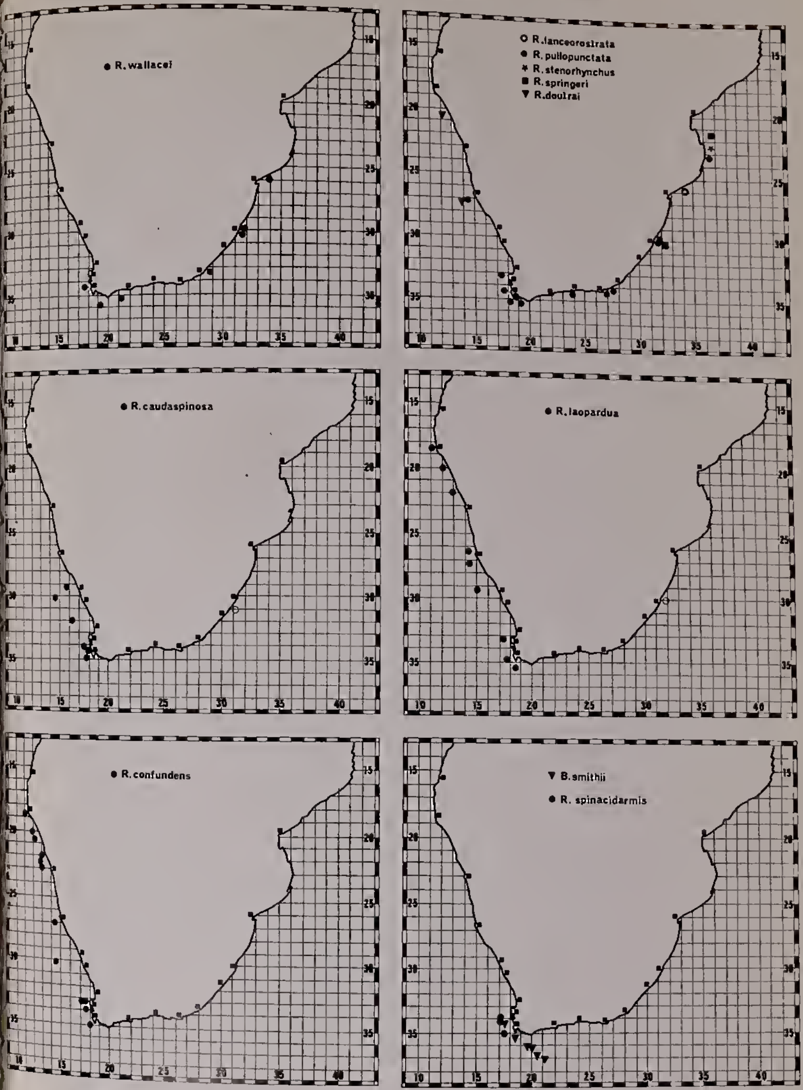

Fig. 59. (*continued*)

While the west/south/east coast distribution of the endemic species, *Cruriraja parcomaculata*, *Raja pullopunctata* and *R. wallacei* (Fig. 59), may be explained in terms of uniformity of temperatures at depths greater than 100 metres, the distribution of the east coast endemics, *Cruriraja triangularis* and *Raja springeri* (Fig. 59), and the west coast endemics, *Raja caudaspinosa* and *R. leopardus* (Fig. 59), are more difficult to account for in terms of temperature dependence. However, both *Cruriraja triangularis* and *Raja springeri* are known only from the northern limits of the east coast (Durban to Barra Falsa) in 230–420 metres and 400–740 metres respectively, where minimum temperatures are higher than further south. *Raja leopardus* and *R. caudaspinosa* are apparently confined to the west coast, west of Cape Point, despite the fact that their type localities have been given as off Durban (Von Bonde & Swart 1923). M. M. Smith (1970) reports an entirely west coast distribution for certain South African fishes, although it appears that this is inexplicable in terms of temperature dependence.

Raja confundens (Fig. 59) is not now regarded as a southern African endemic species, and has been reported at 2°09′N, 9°27′E in 260–650 metres (Krefft 1968*a*; Hulley 1970). Because of this range, it is probable that the species will be taken east of Cape Point in the future.

Bathyraja smithii (Fig. 59) has been recorded from Kerguelen and from the slope regions of the western edge of the Agulhas Bank, where its depth distribution (Fig. 58) indicates an association with the Antarctic Intermediate Water mass. This water mass is characterized by a salinity minimum core (34,33‰) at 600–1 500 metres and temperatures of 4°–5°C (Orren 1963; Shannon 1966), and is sandwiched between the warm Deep Water and Central Water, which forms the source for the Benguela Current. Since the Antarctic Intermediate Water extends northwards in the Indian Ocean at 200–300 metres deeper than in the southern Atlantic (Orren 1963), it is probable that *Bathyraja smithii* is not confined to the western slope regions, and will be taken in depths of 800–1 800 metres off the Natal coast.

In conclusion, it must be pointed out that as far as the southern African rajid fauna is concerned, distribution patterns are complex and do not follow precisely the faunistic provinces as limited by Day (1967), although these limits were based on distribution data only to 200 metres. There is no doubt that tropical West African species extend into this region, but the southern limit of this fauna is indistinct, although inshore species indicate some boundary zone in the region between 18°S and 22°S. Furthermore, while several species seem to be confined to the northern regions of the east coast and indicate another boundary zone in the region south of Durban, i.e. a Natal province, the majority of the species are widely distributed throughout the whole southern African region. There is also some evidence that the direct influence of temperature may not be the only limiting factor.

Summary

The structure of the pelvic girdle, neurocranium and the predorsal caudal vertebral count are described for southern African Rajoidea, as are the structures of the claspers of 17 species of Rajidae, *Rhinobatos annulatus*, *Myliobatis cervus* and *Anacanthobatis marmoratus*, and the North American species *Cruriraja rugosa* and *Anacanthobatis americanus*. A discussion of clasper terminology is included.

On the basis of the above, the southern African Rajoidea have been grouped into the following families, genera and subgenera:

Family **Rajidae**

Genus *Bathyraja* Ishiyama, 1968
  species: *Bathyraja smithii* (Müller & Henle, 1841)

Genus *Raja* Linnaeus, 1758
  subgenus *Raja* Linnaeus, 1758
    species: *R. miraletus* Linnaeus, 1758; *R. clavata* Linnaeus, 1758; *R. straeleni* Poll, 1951
  subgenus *Dipturus* Rafinesque, 1810
    species: *R. doutrei* Cadenat, 1960; *R. pullopunctata* Smith, 1964; *R. lanceorostrata* Wallace, 1967; *R. springeri* Wallace, 1967; *R. stenorhynchus* Wallace, 1967
  subgenus *Rostroraja* subgen. nov.
    species: *R. alba* Lacépède, 1803
  subgenus *Amblyraja* Malm, 1877
    species: *R. radiata* Donovan, 1808; *R. robertsi* Hulley, 1970
  subgenus *Leucoraja* Malm, 1877
    species: *R. wallacei* Hulley, 1970
  subgenus *Rajella* Stehmann, 1970
    species: *R. caudaspinosa* Von Bonde & Swart, 1923; *R. leopardus* Von Bonde & Swart, 1923; *R. confundens* Hulley, 1970; *R. dissimilis* Hulley, 1970; *R. ravidula* Hulley, 1970

Family **Crurirajidae** fam. nov.

Genus *Cruriraja* Bigelow & Schroeder, 1948
  species: *C. durbanensis* (Von Bonde & Swart, 1923); *C. parcomaculata* (Von Bonde & Swart, 1923); *C. triangularis* Smith, 1964

Family **Anacanthobatidae**

Genus *Anacanthobatis* Von Bonde & Swart, 1923
  species: *A. marmoratus* Von Bonde & Swart, 1923

Genus *Springeria* Bigelow & Schroeder, 1951
  species: *S. ori* Wallace, 1967

The subgenus *Rostroraja* is described as new and includes the single species, *Raja alba*, while a new family, Crurirajidae, is defined to include all species of the genus *Cruriraja*. The family Anacanthobatidae is diphyletic and, for the moment, it is considered that the genus *Anacanthobatis* is monotypic. The North American species *Anacanthobatis americanus* should be referred to a new genus.

The phyletic interrelationships of the suborder Rajoidea, based on these morphological details, are discussed and an evolutionary pattern, different from that of Stehmann (1970), is proposed. On this evidence, and on the evidence presented by world-wide zoogeographical distribution, a theory as to the origin of the southern African rajid fauna is advanced. The effectiveness of a warm-water barrier zone off the East African coast and its prevention of either a northward migration of temperate rajid species or a southern invasion by Indo-Pacific species appears to be significant and is discussed in relation to the origin of the rajid fauna.

The distribution of the southern African Rajidae is discussed with particular reference to temperature parameters, so far as the limited data will allow.

ACKNOWLEDGEMENTS

I am deeply indebted to Dr N. A. H. Millard, formerly of the Department of Zoology, University of Cape Town, for helpful criticism and guidance throughout this work, and to Mr S. X. Kannemeyer, of the South African Museum, for his assistance during all phases; to Dr G. Krefft, Institut für Seefischerei, Hamburg, for many suggestions and valuable criticism and for much useful material; to Dr M. Stehmann, Institut für Seefischerei, for many inspiring discussions and recommendations; and to Prof. R. Ishiyama, Tokyo University of Fisheries, for his advice.

I am grateful to the late Prof. J. L. B. Smith and Mrs M. M. Smith, J. L. B. Smith Institute of Ichthyology, Grahamstown; to Mr J. H. Wallace, Oceanographic Research Institute, Durban; and to the Directors of the British Museum (Natural History), the Institut für Seefischerei, the Institut Royal des Sciences Naturelles de Belgique and the Muséum National d'Histoire Naturelle, for access to their collections.

I wish to express my thanks to Mr Stewart S. Springer, formerly of the National Museum of Natural History, Washington, not only for many X-ray photographs, but also for the donation of specimens of *Anacanthobatis americanus* and *Cruriraja rugosa*; to Dr F. M. Mombeck, Institut für Seefischerei, for the collection of the *Walther Herwig* specimens; and especially to Miss Christa Lübben, Institut für Seefischerei, for photographs and X-ray plates of *Raja straeleni* and *R. spinacidermis*, and for her kind hospitality during my stay in Hamburg.

My thanks are also due to the following individuals, either for placing specimens in existing collections at my disposal or for help with X-ray photography: Miss P. Verity, Nuffield Institute for Comparative Medicine; Drs P. H.

Greenwood, N. B. Marshall and Mr A. Wheeler, British Museum (Natural History); Dr W. Templeman, Fisheries Research Board of Canada, St. Johns; Dr J. P. Gosse, Institut Royal des Sciences Naturelles de Belgique, Brussels; Dr M. Poll, Musée Royal d'Afrique Centrale, Tervuren; Dr M. L. Bauchot, Muséum National d'Histoire Naturelle, Paris; Messrs M. J. Holden and C. N. Humphries, Fisheries Laboratory, Lowestoft; and Drs H. Wormald and R. Hindle, Durban.

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